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The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini)

PAUL H. WILLIAMS

c/o Department of Entomology, British Museum (Natural History), Cromwell Road, South Kensington, London SW7 5BD

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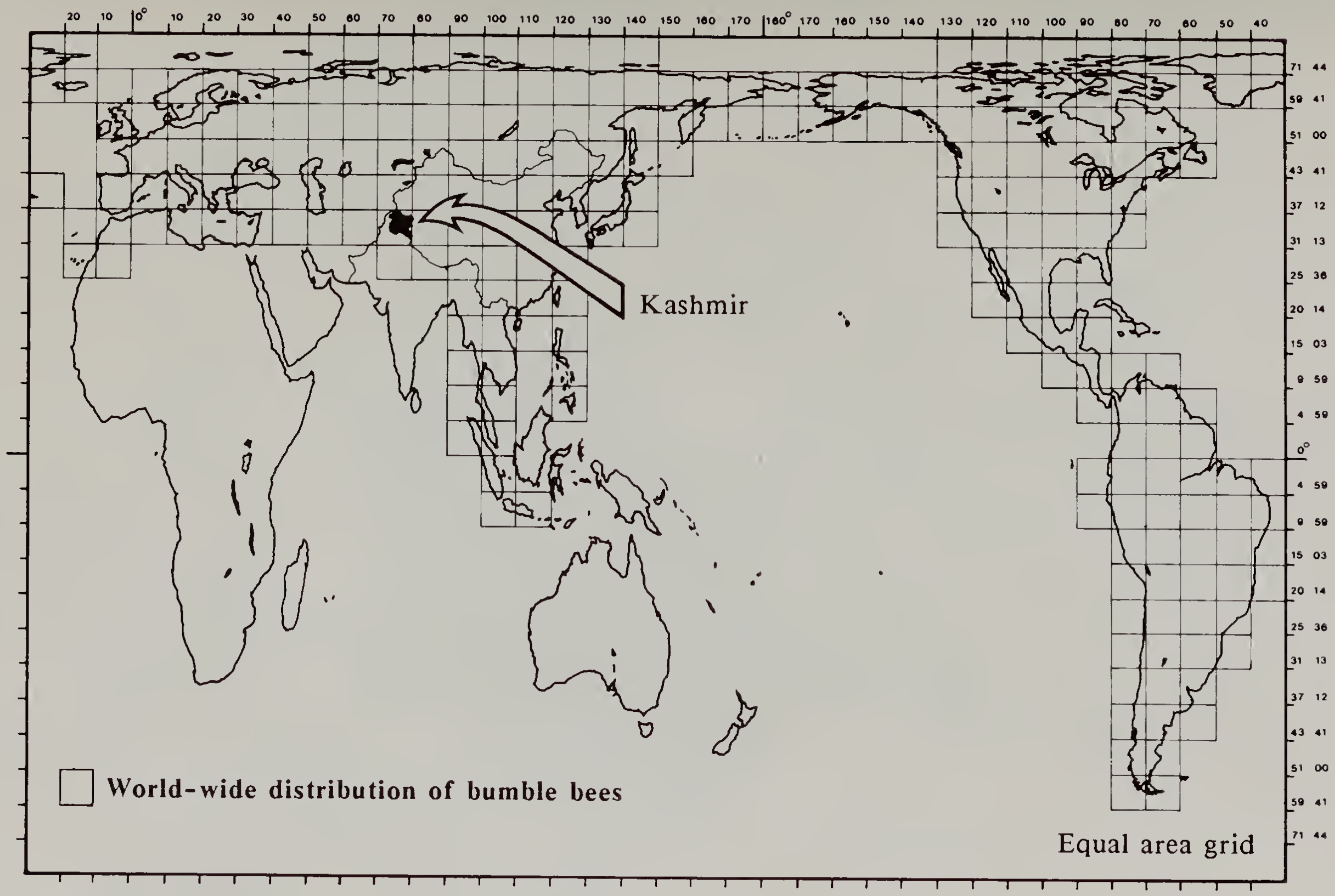
SYNOPSIS. Bumble bees are extraordinarily variable in the colour patterns of their pubescence. This has contributed to the lack of agreement among authors concerning the discrimination of species. Material from Kashmir has been listed previously under 80 names, but for the broadest interpretations of these species, more than 500 names have been published for differing individuals from throughout their distributions. In this review, all of the available voucher material from Kashmir (6312 museum specimens from 78 sites) is assigned to just 29 species. The reduction in the number of nominal taxa that are inferred to represent separate species depends on two factors. First, variation is examined among the larger samples of new material. Second, current species concepts require a re-assessment of this evidence for the limits of reproductive cohesion in space and time. A particular study is made of the variation in male mate-searching behaviour and of its relationship to the different kinds of habitat. For *Bombus asiaticus*, patterns of colour variation across the Great Himalaya are compared with those expected from simple genetic models. Type material is examined for 103 of the nominal specific and subspecific taxa. Seventeen lectotypes are designated and 80 new synonyms and provisional new synonyms are established. Keys to the species are accompanied by diagrams of the colour patterns and by distribution maps.

INTRODUCTION

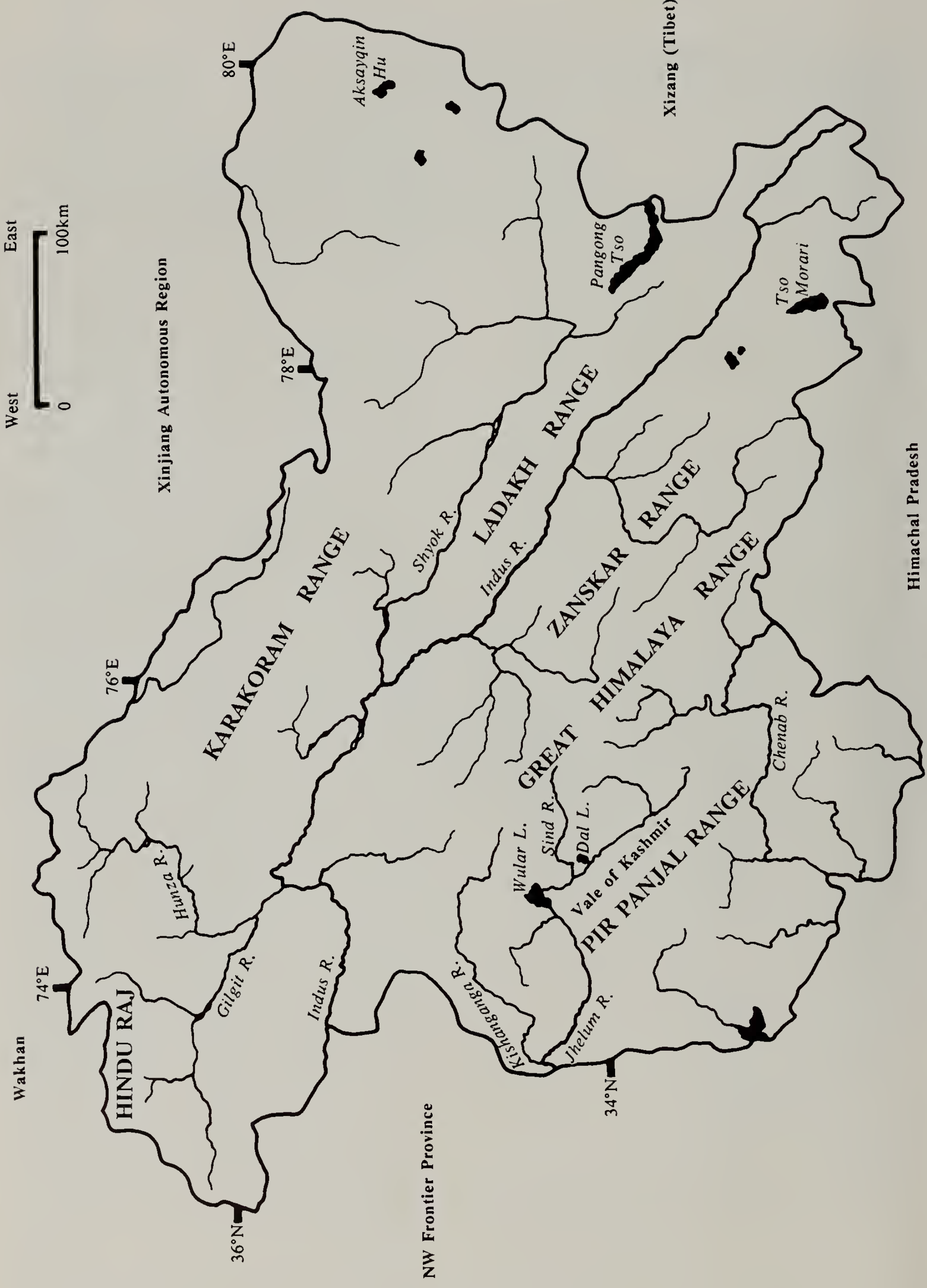
Bumble bees rank among the most abundant and conspicuous of flower visitors in alpine, temperate and arctic environments of the northern continents. In the southern hemisphere they are native only in the East Indies and South America (see Map 1), where most species are associated with the highlands. Adults feed mainly on nectar, which provides energy for flight. The larvae are fed on a mixture of pollen and honey, which provides their requirements for growth. Most species are social (reviews of behaviour by e.g. Alford, 1975; Morse, 1982; Plowright & Laverty, 1984). The colonies consist almost always of a single, mated queen, which lays most of the eggs, and usually of no more than a few hundred, unmated workers. The establishment and development of colonies takes place each summer and may take less than two months (Richards, 1973), culminating with a switch to the production of males and young queens near the end of the season. After mating, young queens normally diapause through the winter, away from the nest, before they attempt to found colonies on their own in the following year. Only a few species from the tropics of South America (Sakagami, 1976) and South East Asia (Michener & Amir, 1977) may have colonies that persist for more than one year. Bumble bees show unusually well-developed endothermy, which can be facultative when foraging (reviewed by Heinrich, 1979). Almost all species are generalists in their choice of food-plants, visiting any remunerative flowers. Their foraging follows a 'scramble' pattern, without either recruitment of nest-mates to good food sources or defence of food sources. These characteristics of bumble bees may account for their abundance in cool environments that have a predictable season of adverse conditions, where flowers are often fairly evenly dispersed. In contrast, the other social, long-proboscis bees (honey bees and stingless bees) have their centres of diversity and abundance in the tropical lowlands.

The bumble bees of Kashmir are of particular interest because this narrow corridor of mountains is almost the only major, modern point of contact between the large and divergent Oriental and Palaearctic bumble bee faunas. These faunas are otherwise separated by deserts in central Asia and in China, except for another corridor of contact near Beijing, which is occupied by relatively few species (Panfilov, 1957). Greater Kashmir encompasses almost the entire mountain system that links the high Tibetan (Xizang-Qinghai) plateau in the east with the Hindu Kush, Pamir and Tien Shan mountain ranges to the west and north. Hence Kashmir covers segments of the Pir Panjal, Great Himalaya, Zanskar, Ladakh, Karakoram and Hindu Raj ranges (Map 2), and includes some of the highest peaks in the world (altitudes range between about 400–8600 m; for an account of the geological structure see Searle *et al.*, 1988). Kashmir is slightly larger in area than the European Alps and lies at the same latitude as Syria, Tunisia and Arizona. Since Indian independence in 1947, the sovereignty of Kashmir has been a matter of dispute and sections are now administered by India (Jammu & Kashmir State), Pakistan (Northern Areas) and China (as part of the Xinjiang Autonomous Region).

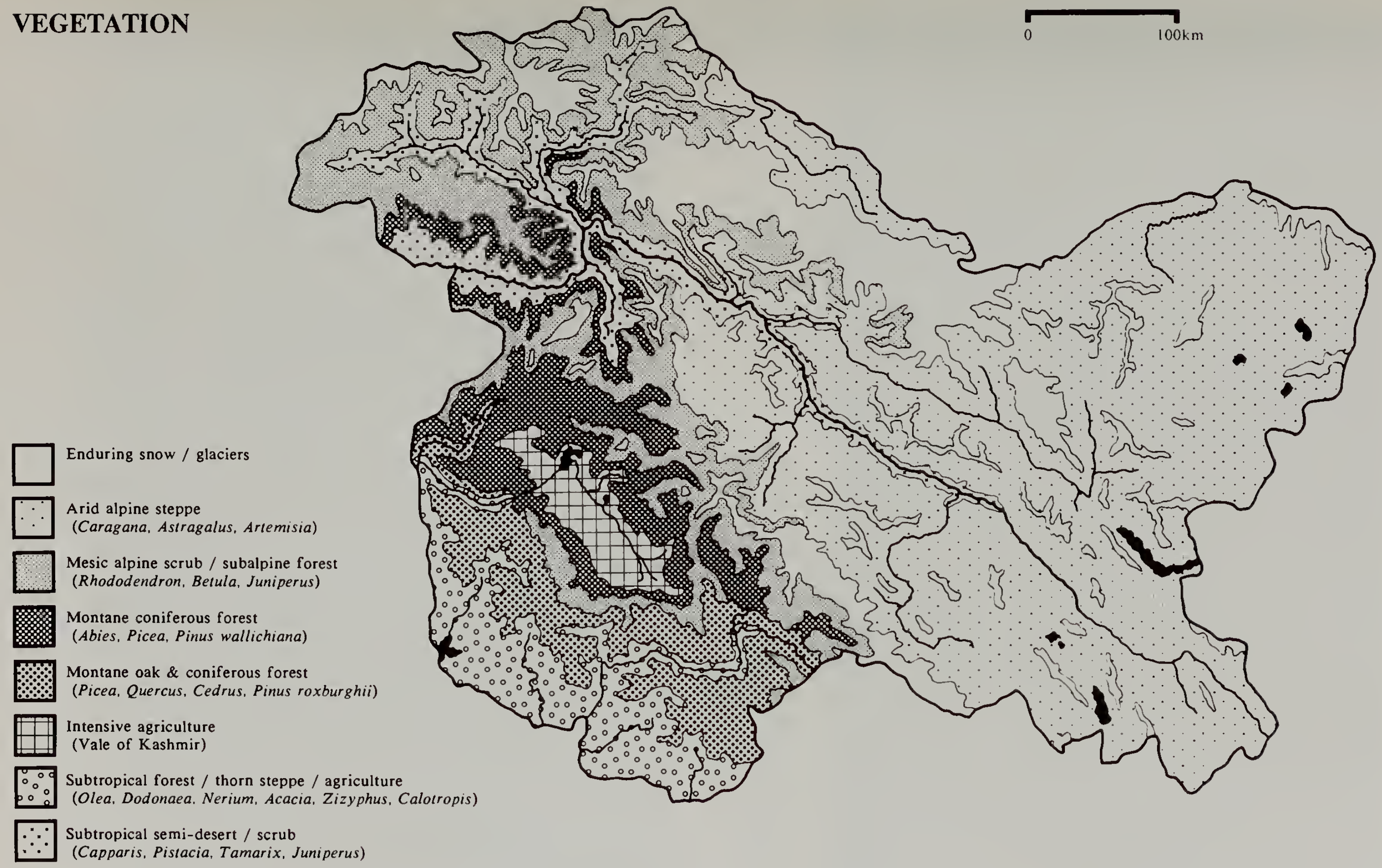
The high relief of Kashmir provides a broad range of habitats for bumble bees. Patterns in the distributions of bumble bees in Europe have been linked with climatic factors (e.g. Pekkarinen *et al.*, 1981). The differing climates of Kashmir can be summarised in three regions (e.g. Gurcharan Singh & Kachroo, 1976). First is the subtropical region of the Jammu foothills, which is subject to the summer monsoon (Fig. 2). Second, beyond the Pir Panjal range, is the more temperate Vale of Kashmir, where most of the rain and snow fall in the winter months (Fig. 1). Third, in the rain shadow of the Great Himalaya, is the arid alpine region of the Zanskar, Ladakh and Karakoram ranges (Figs 3 & 4). But of equal importance to climate, as an influence on whether or not a species of bumble bee could persist at a particular locality, may be the nature of the local vegetation (e.g. Bowers, 1985; Williams, 1988, 1989), even though bumble bees are seldom dependent on particular species of food-plants. Map 3 shows a summary of the vegetation in Kashmir, based on the survey of the Himalaya by Schweinfurth (1957). Not only do the three principal climatic regions within Kashmir differ in their flora, but in combination with the influences of local altitudinal zonation and variation in local exposure (Troll, 1972), this contributes towards a particularly broad range of habitats. In comparison with some parts of the Himalaya, Kashmir retains relatively



Map 1 Position of Kashmir (in black) in relation to the known, native distribution of all bumble bees, which is shown covered by the grid. This map uses a cylindrical equal-area projection that is orthomorphic at 45° N/S, where bumble bee records are particularly numerous. The grid is calculated from intervals of longitude of 10°. The area covered by the grid in Central and South America may be a slight over-estimate of the distribution of bumble bees there.



Map 2 Principal mountain ranges and rivers of Kashmir in the broad sense.



Map 3 Summary of the vegetation that predominates in the different regions of Kashmir (adapted from Schweinfurth, 1957). Much of the area at lower altitudes (see Map 4) is heavily exploited for agriculture.

Fig. 1 Subalpine zone of Mt Apharwat in the Pir Panjal range, viewed from 3000 m towards the peak at 4143 m (Map 4 locality 1: foreground pasture with *Euphorbia wallichiana*; lower slopes dominated by *Betula utilis*, *Salix* sp., *Syringa emodi*, with a few *Abies spectabilis*; middle slopes dominated by *B. utilis*, *Rhododendron campanulatum*; higher slopes dominated by *R. anthopogon*, *Juniperus recurva*). Of 17 species of bumble bees recorded in this immediate area, the most restricted to this zone is *B. biroi*, and the most abundant is *B. rufofasciatus*.

Fig. 2 Lower montane coniferous forest zone on the Patnitop ridge in the Jammu foothills, viewed from 2000 m towards the plains of India (Map 4 locality 11: Patnitop dominants, *Cedrus deodara* [foreground], *Pinus wallichiana*, *P. roxburghii*). Of 3 species of bumble bees recorded in this area, the most restricted to this zone is *B. haemorrhoidalis*, and the most abundant is *B. trifasciatus*.

Fig. 3 High, arid alpine steppe zone at the terminal moraine of Nimaling plain in the Zanskar ranges, viewed from 4800 m across the southern lateral moraine towards a peak (Kang-y-sey) at 6400 m (Map 4 locality 51: foreground, shrubs of *Caragana versicolor*). Of 9 species of bumble bees recorded in this immediate area, the most restricted to this zone are *B. personatus*, *B. oberti* and *B. ladakhensis*, of which the most abundant is *B. oberti*.

Fig. 4 Subalpine semidesert zone at Lamayuru near the Indus valley, with a view of valley terraces at 3400 m, against a background of mountain ridges at 4000–5000 m (Map 4 locality 42). Of 3 species of bumble bees recorded in this area, the most restricted to this zone, and the most abundant, is *Bombus semenovianus*.

large forests and yet access to some of the varied alpine areas is no longer difficult.

Previous studies of the bumble bees of Kashmir have been based on a total sample of only a couple of hundred specimens. The first important collection of bumble bees from Kashmir was made by Lt.-Col. C. G. Nurse in 1901. A complete inventory of this material was never published, although it provided the specimens that have since been described as the types of many nominal taxa (Friese, 1909, 1918; Richards, 1928*a*, 1928*b*, 1930; Tkalců, 1974*b*). Other collections were mostly small, but particularly important material was obtained by A. Jacobson in Kashmir and Ladakh during 1912 (Skorikov, 1914*a*) and by Col. R. Meinertzhagen in Ladakh during 1925 (Richards, 1928*b*). Skorikov (1933*b*) compiled a preliminary list of the fauna of Kashmir and discussed the fauna of the entire Himalaya, though his work was based on a different concept of the species from that accepted at present. The only recent revision of any part of the large Himalayan fauna is Tkalců's (1974*b*) description of a collection of 73 bumble bees from Nepal. Although there are many elements in common between the faunas of Nepal and Kashmir, 16 species that are known from Kashmir are not represented in this collection. In the same paper Tkalců refers to his '*Monographie der Unterfamilie Bombinae des Himalaya*' as in press. Unfortunately this has never been published, although recently he has described several new taxa from the region (Tkalců, 1989). The only key that has been intended to cover any part of the Himalayan fauna is that published by Bingham (1897). This key artificially subdivides four of the species now recognised from Kashmir, whereas a further 20 species are not included at all.

For this review, much of the older material is re-examined and compared with the larger collections of new material, in order to describe some of the patterns of variation (and the discontinuities in these patterns) among the bumble bees of Kashmir. This evidence, together with information from the habitat associations of the species in Kashmir and information from their broader distributions beyond Kashmir, is used to discuss the likely relationships of ancestry and interbreeding among the nominal taxa.

Table 1 Localities that have been sampled for bumble bees. Sites in close proximity are treated as combined and represented by a single number on Map 4.

Localities from which samples of bumble bees have been examined (numbers in circles on Map 4).

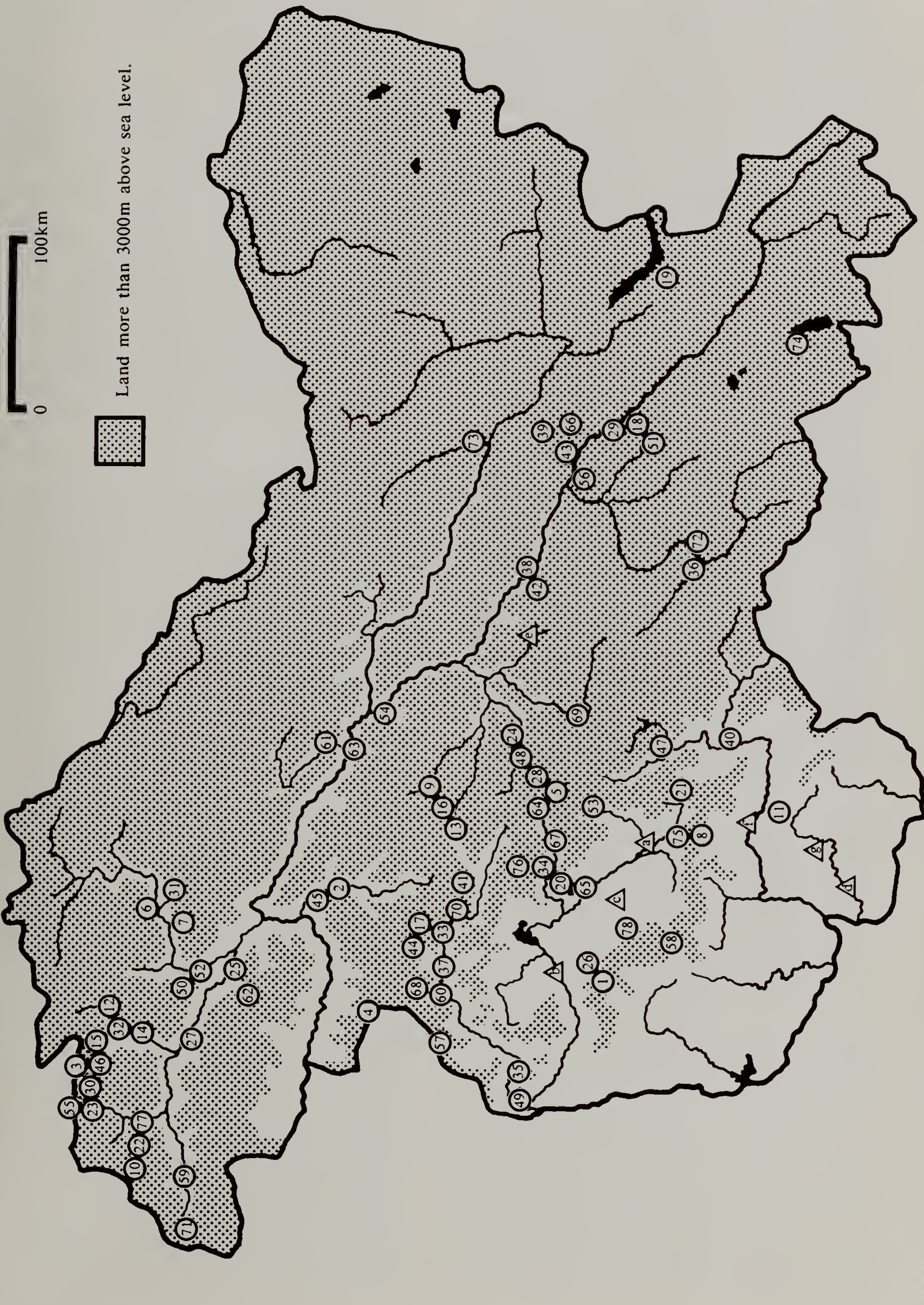
1 (Mt) Apharwat
2 Astor
3 Atro Sar
4 Babusar
5 Baltal
6 Baltit
7 Banidas
8 Banihal
9 Bara Deosai
10 Batakush
11 Batote
12 Bulandi
13 Burzil Chauki
14 Chakorkhand
15 Chhantir Gah
16 Chhota Deosai
17 Chittakatha Sah
18 Chogdo
19 Chushul
20 Dachhigam
21 Daksum
22 Dalti
23 Darkot
24 Dras
Gamelti = Darkot
25 Gilgit
26 Gulmarg
27 Gulmiti
28 Gumri
Harwan = Dachhigam
29 Hemis
30 Holojut
31 Holshal
Hunza = Baltit
32 Imit
33 Janwai
34 Kangan
35 Kanur
36 Karsa
37 Kel
38 Khalsi
39 Khardung La
Khilanmarg = Apharwat
40 Kishtwar
41 Lal Pani
42 Lamayuru
43 Leh
44 Lilam
45 Luskum
46 Mahthantir Gah
Martselang = Chogdo
47 Maru
48 Matayan
49 Muzaffarabad
Nagar = Holshal
50 Naltar
Nigagar = Baltal
51 Nimaling
52 Nomal
Nowgam = Banihal
53 Pahalgam
54 Parkutta
Patnitop = Batote
55 Rawat
56 Rumbak
57 Saif-ul-Maluk Sar
58 Sangisfaid
59 Shamran
60 Shardi
61 Shigar
62 Shinghai Gah
63 Skardu
64 Sonamarg
65 Srinagar
66 Stakmo
67 Sumbal
68 Surgun
69 Suru
Tangmarg = Gulmarg
70 Taobat
71 Teru
Thajiwas = Sonamarg
72 Thonde
73 Tiggur
74 Tso Morari
Tungri = Karsa
75 Verinag
76 Wangat
77 Yasin
78 Yusmarg
Zoji La = Gumri

Localities at which no bumble bees could be found during brief surveys in August–September 1980, 1985 or 1986 (letters in triangles on Map 4).

a Anantnag
b Baramula
c Chrar-i-Sharif
d Jammu
e Mulbekh
f Ramban
g Udhampur

MATERIAL EXAMINED AND DEPOSITORIES

Large samples of undescribed material are available from western Kashmir in the collections



Map 4 Localities from which material has been examined (numbers in circles) or at which no bumble bees could be found (letters in triangles). See Table 1 for locality names.

made during 1953 and 1954 by F. Schmid (BMNH accession 1962–457; account of the expedition in Schmid, 1958). In addition, I was able to make large, selective collections from southern and eastern Kashmir during 1980, 1985 and 1986. Unfortunately, large areas near the borders, especially to the north and east of the country, are prohibited to foreign visitors, so only a few specimens from older collections are available.

The sites in Kashmir from which material has been examined are listed in Table 1 and shown on Map 4. Geographical information is taken from the United States Survey of India maps (scale 1 : 250,000) and from The Times atlas of the world (1987). The world-wide distribution of species is also shown by maps (see Map 1). These are compiled with a preference for records from those specimens that I have been able to examine, supplemented by a list of selected references. The source material is summarised briefly in the text either by political region (for the Himalayan/Tibetan mountain system in India and China) or by major mountain system (for the more restricted bumble bee faunas of central Asia), such as the Elburz, Hindu Kush, Pamir, Alai – Tien Shan (in its broadest sense) and Altai mountains. More precise data can be found in the original references. The specimens that have been examined are deposited in collections as shown by the references to the following abbreviations.

AB	Dr A. A. Bhat, S.K. University of Agricultural Sciences & Technology, Srinagar, India.
BMNH	British Museum (Natural History), London, U.K.
BPBM	Bishop Museum, Honolulu, U.S.A.
BT	Dr B. Tkalců, Prague, Czechoslovakia.
FA	Faculté des Sciences Agronomiques de l'Etat, Gembloux, Belgium.
INHS	Illinois Natural History Survey, Champaign, U.S.A.
ITZ	Instituut voor Taxonomische Zoölogie, Amsterdam, Netherlands.
IZ	Institute of Zoology, Beijing, China.
LK	Dr L. S. Kimsey, University of California, Davis, U.S.A.
LSL	Linnean Society, London, U.K.
MCSN	Museo Civico di Storia Naturale, Genoa, Italy.
MI	Dr M. Ito, Hokkaido University, Sapporo, Japan.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MNHU	Museum für Naturkunde an der Humbolt-Universität, Berlin, D.D.R.
NM	Naturhistorisches Museum, Vienna, Austria.
NMP	Národní Muzeum, Prague, Czechoslovakia.
NMS	Natur-Museum Senckenberg, Frankfurt, D.B.R.
NR	Dr N. D. Rishi, University of Kashmir, Srinagar, India.
PW	Author's collection, London, U.K.
RH	Dr R. W. Husband, Adrian College, Adrian, U.S.A.
SEMK	Snow Entomological Museum, Lawrence, Kansas, U.S.A.
TL	Dr T. M. Laverty, University of Western Ontario, London, Canada.
TM	Természettudományi Múzeum, Budapest, Hungary.
UM	University Museum, Oxford, U.K.
USNM	United States National Museum, Washington D.C., U.S.A.
ZI	Zoological Institute, Leningrad, U.S.S.R.
ZM	Zoologisk Museum, Copenhagen, Denmark.
ZMMU	Zoological Museum of Moscow State University, Moscow, U.S.S.R.
ZS	Zoologische Staatssammlung, Munich, D.B.R.

DIAGNOSIS OF HIMALAYAN BOMBINI

Among the Apidae, the Bombini have the labrum at least twice as broad as long. The labrum lacks a longitudinal median ridge, although for the females it has a strong transverse basal depression. The clypeus has a transverse subapical depression and the apico-lateral corners are curved back towards the occiput. A malar area (= malar space) separates the compound eye from the base of the mandible, often by a distance greater than the breadth of the mandible at its base. The hind wings lack a jugal lobe (= anal lobe). The volsella (= lacinia) of the male genitalia is greatly enlarged and is produced apically beyond the gonostylus (= squama).

Bumble bees are large (body length 7–27 mm) robust insects. Their bodies have a dense covering of variously-coloured long plumose hairs, although these are few or absent on some parts of the ventral surface of the gaster, on parts of the propodeum, on parts of the anterior face of gastral tergum I, and on parts of the head. The sclerites are usually black, or lighter brown on the distal parts of the limbs, but are never marked with bright yellow, red, or metallic (= interference) colours. The wings may be transparent (= hyaline) to strongly darkened (= infuscated), but rarely show strongly metallic reflections.

Female bumble bees have 12 antennal 'segments' (= scape, pedicel and 10 flagellomeres) and six visible gastral terga and sterna (abbreviated to TI-VI, SI-VI). Males have 13 antennal 'segments' (=

scape, pedicel and 11 flagellomeres) and seven visible gastral terga and sterna (abbreviated to TI-VII, SI-VII).

CHARACTERS STUDIED

Although this review aims to describe many aspects of variation among the bumble bees of the Kashmir Himalaya, inevitably those characters that vary most among species and least within species receive most attention. Many characters of the females show more pronounced expression and divergence among the queens (which are usually the larger females) than among the workers (smaller females).

The most variable characters of bumble bees are the colours of their pubescence. These are so variable that they can be very misleading if used alone for the identification of species. For instance, it is known that in some areas of Europe and North America the local parts of populations from even very divergent species-groups appear to have converged closely in colour pattern (see the comments on discrimination of species and intraspecific variation, and the discussion of colour patterns of the Kashmir fauna). Differences in the shape and sculpturing of the sclerites have been found to be more reliable indicators of relationship.

On the head, the shape and details of the sculpturing of the LABRUM, CLYPEUS and MALAR AREA (= oculo-malar space) are frequently used as characters (Fig. 14). The superficial structure and sculpturing of the labrum may be particularly complex (Figs 23–30, 220–222). The shape of the malar area can be measured as the ratio of the oculo-malar distance to the breadth of the mandible at its base (Fig. 15). This shape is related to variation in proboscis length (Medler, 1962), which is in turn related to variation in the behaviour governing flower choice, both among and within species (reviewed by e.g. Morse, 1982). However, within at least some of the species with longer proboscides, the shape of the malar area may be subject to allometric effects among individuals of different sizes (e.g. Sakagami, 1972). Furthermore, because the boundaries of the malar area require arbitrary definition, measurements by different authors are not always comparable. Therefore this character is used here only when the differences in shape are relatively large. The MANDIBLES provide many characters including the number and shape of the ridges known as KEELS, between which are grooves, such as the SULCUS OBLIQUUS (Figs 31–38). There is a BASAL TOOTH, variable numbers of subsidiary or INTERCALARY TEETH and often an APICAL TOOTH, which is defined at its base by an anterior notch known as the INCISURA. These characters vary within species as well as among them and are subject to further apparent variation caused by wear. Nonetheless, they can still be useful in some species-groups (e.g. the subgenera *Psithyrus*, *Alpigenobombus*). The shape of ANTENNAL 'SEGMENTS' (= scape, pedicel and flagellomeres), measured as ratios of length to breadth, is also used here, but only when the differences in shape are large (Figs 17–22, see the comments above on the shape of the malar area). The OCELLI vary in size and in position relative to the compound eyes. The separation of the lateral ocellus from the neighbouring margin of the compound eye can be measured in relation to the diameter of the lateral ocellus (Fig. 16). The strongly enlarged ocelli of the females of some species are associated with enlarged compound eyes among the conspecific males, and hence with particular kinds of male mate-searching behaviour (see the comments on mate-searching behaviour of male bumble bees in Kashmir). One of the characters most prone to variation, both within and among species, is the sculpturing of the OCELLO-OCULAR AREAS of the VERTEX (= frontovertex), on the top of the head (Figs 215–219). Just as for variation in the sculpturing of the labrum and clypeus, some of the elements in the patterns of punctures of the ocello-ocular areas are constant among large groups of species, whereas other details are subject to variation among individual bees from the same colony.

On the thorax, the majority of characters are taken from the appendages (Fig. 43). Subtle differences in the shape of the wing venation have occasionally been used (e.g. Milliron, 1971; Plowright & Stephen, 1973), although these are not easy to measure (see the comments above on the malar area). Above the wing bases are a pair of small dome-shaped TEGULAE, which are shown in the colour pattern diagrams. Between the tegulae, on the thoracic dorsum, is the SCUTUM (= mesoscutum), and immediately posterior to it, the SCUTELLUM (= mesoscutellum). These sclerites show some variation in sculpturing (Figs 223 & 224), but are also useful for relating to the distribution of pale or black pubescence. The relative length of the pubescence on various parts of the legs can be used to measure the general length of the pubescence of the body (e.g. by comparison with tibial breadth). The outer surface of the hind TIBIA has large areas without long pubescence for females of most species, although to a lesser extent for females of the subgenera *Psithyrus* and *Mendacibombus* and for males of some other species (Sakagami & Ito, 1981). For these females the bare areas are surrounded by dense fringes of long, stout hairs that function as a CORBICULA for carrying pollen. Variation in the length and extent of this pubescence and in the sculpturing of the bare areas have been used to distinguish taxa (Figs 225 & 226), although there can be considerable differences between queens and workers within the same species (see the comments on *B. simillimus*). Among some species-groups there is a pronounced development of the disto-posterior corners of the hind tibia and of the mid and hind BASITARSI (= first tarsomeres) (Figs 39–42). These can form spinose projections, but differences between closely-related species are seldom discrete. The shape, sculpturing and pubescence of the hind basitarsus are also used (Figs 227–229).

On the abdomen, the most obvious characters are found in the variation of the sculpturing of the sclerites. Bumble bees, like other Apocrita, have a waist between the first two abdominal segments, so that the first abdominal segment (= propodeum) is associated with the thorax, whereas the subsequent segments form a separate unit, the GASTER (= 'metasoma'), which can be moved independently. In this review all references to segment numbers for the dorsal TERGA (= tergites) and ventral STERNA (= sternites) refer to gastral segments, so gastral tergum I is the dorsal sclerite of the second abdominal segment. For the females, variation in sculpturing is often especially clear on gastral tergum VI (= epipygium or pygidium) and sternum VI (= hypopygium), which may also show single or double KEELS (= ridges) (Figs 206–211), or even a rounded boss, as well as variation in the shape of the apex (Figs 212–214, 230, 231). There is some variation in the structures associated with the female STING (= modified ovipositor), especially in the shape of the 'inner projections from the sting sheath' (Richards, 1927*b*, 1968; see also Kopelke, 1982). However, many of the 'sting sheath' characters are parts of the folds that lie between the rami of the left and right valvulae (see Williams, 1985: fig. 5) and these folds are usually only weakly sclerotised. Consequently they do not always preserve well in dried specimens and may become distorted, so these characters are not used here. In contrast, the male GENITALIA (= genital capsule) do preserve well because they are strongly sclerotised and so require no treatment other than a straightforward extraction from the gaster with a pin. The male genitalia consist of a pair of gonoforceps for clasping the female and an intromittant organ (Figs 44 & 45). During pairing, the female is locked with her sting assembly pulled posteriorly and dorsally away from the male (Williams, 1985: fig. 5) by at least three points of contact: (1) the VOLSELLAE (= laciniae, but see the discussion below) press the sting base from above and (2) the GONOSTYLI (= squamae) hold the rami of the female valvulae with an opposing action from below, so that the sting base is gripped; at the same time, (3) the apex of the female's sternum VI is gripped between the male's parapenial processes of the GONOCOXITES (= stipes) and the base of the SPATHA, ensuring that the sting assembly is clamped in a protruded position, which gives access to the female gonopore for the male intromittant organ. Kopelke (1982) describes how the PENIS VALES (= sagittae) anchor among the weakly sclerotised folds that lie between the rami of the valvulae of the female sting base. Many of these structures of the male genitalia show complex elaborations that are particularly valuable taxonomic characters (Figs 46–205, see the comments on relationships among species by ancestry). For the males, gastral sternum VIII and sternum IX (= subgenital plate) are found below the genital capsule and are normally retracted above sternum VII. Variation in their shape and pubescence has been described by many authors. This variation may also be great even within species and it is often accompanied by a pronounced overlap in variation among related species. Consequently these characters are not used here.

There has been some disagreement as to the homology of the 'lacinia' of male bumble bee genitalia, concerning whether it is derived from part of the volsella or from part of the gonostylus (e.g. Snodgrass, 1941; Smith, 1970). As yet no study of ontogeny has been sufficiently detailed to establish its homology conclusively, so the interpretation depends on comparative studies of the morphology of adults. Zander (1900) did study the ontogeny of male bumble bee genitalia and concluded that a small scale ('Schuppe') on the inner ventral surface of the gonocoxite is of volsellar origin because it is in the expected position and becomes strongly chitinised early in development. However, he made no detailed observations on the derivation of the larger ventral structure known as the 'lacinia'. Later Smith (1970) concluded from their topological similarity that the ventral scale is derived from the digitus of the ancestral volsella, but that the larger ventral structure known as the 'lacinia' is derived from the cuspis of the ancestral volsella. Snodgrass (1941) had argued that Zander's scale is the only expression of the volsella and that the large ventral 'lacinia' is derived from the ventral lobe of the gonostylus. He supported this argument with the observation that the 'lacinia' is connected with the dorsal gonostylus for part of its length by a membrane. However, against this argument it must be noted firstly that some bees, including centrines such as *Epicharis rustica* (Olivier) and euglossines such as *Eufriesea pulchra* (Smith), clearly show both major lobes of the gonostylus as well as a third large ventral sclerite in a similar position to the base of the 'lacinia' of bumble bees, below the inner ventral margin of the gonocoxite (see Fig. 5). Therefore this 'lacinia' cannot be the ventral lobe of the gonostylus, although it is in a reasonable position to be part of the volsella and appears to be distinct from Zander's scale. Secondly, among these bees with a bilobed gonostylus, the two lobes are clearly strongly fused near their bases, which is not known between the gonostylus and the 'lacinia' for any bumble bees, which have only the weakly sclerotised membrane noted by Snodgrass. Traces of the two lobes of the gonostylus may be retained among bumble bees as the distal lobe and the interio-ventral process, although these are reduced among species of the subgenus *Mendacibombus* and among many euglossine bees. Thus in the absence of a more detailed ontogenetic study, the weight of evidence supports the argument that a volsellar derivation for the 'lacinia' is most likely.

RELATIONSHIPS AMONG SPECIES BY ANCESTRY

The bumble bees, including the 'cuckoo' bumble bees, form an easily recognised and monophyletic (sensu Hennig, 1981) group of about 240 species (present estimate). Their closest relatives are believed to be the South American orchid bees, the Euglossini (Winston & Michener, 1977; Kimsey, 1984), which have been used in the cladistic analyses for out-group comparisons. Opinions differ concerning the relationships among the many described species-groups of bumble bees, so that many specialists working with bumble bees currently follow their own individual supraspecific classifications.

The present ideas of relationship among species of bumble bees are revised and developed from those proposed in a preliminary cladistic analysis of the functional characters of the male genitalia (Williams, 1985). In practice, most authors since Schmiedeknecht (1882) and Radoszkowski (1884) have used differences in characters of the male genitalia to recognise species-groups among bumble bees. Richards (1968) reviewed the variation in morphology among these established groups and provided diagnoses that also include other characters from both sexes. More recently, Ito (1983, 1985) compared similarities between the male genitalia of species in these groups in a detailed phenetic study.

Some criticism has been made of the classification of bumble bees primarily by characters of the male genitalia because it relies on such a restricted character set. But the characters of the male genitalia that function in clamping the male to the female for copulation (see the comments on characters studied) are especially suitable for use in classification not only because they present many different character states but also because there appears to be a particularly high congruence in the patterns of these character states among taxa (Williams, 1981, 1985). The evolutionary interpretation of the high congruence in the patterns of character states of bumble bee genitalia is that there is relatively little homoplasy among these characters. The classification of flowering plants has long been based on characters of their genitalia for similar reasons.

Evolutionary explanations for why male genitalia are often so strongly differentiated among species have included those that depend on a principal role for the genitalia as a species-isolating mechanism (the lock-and-key hypothesis, reviewed by Shapiro & Porter, 1989), or as a mechanism for female arousal (the stimulation hypothesis, see Eberhard, 1985), or as an impregnable holdfast mechanism (see below). From a study of bumble bee morphology, Richards (1927*a*, 1927*b*) concluded that at least in their case mechanical incompatibility is unlikely to have evolved as an isolating mechanism (see also the comments on the biological species and the Recognition Concept). At that time Richards had apparently not actually observed how the genitalia fit together during pairing between bumble bees, because he referred to Boulangé (1924) for a description of a pinned pair of *B. hortorum* (L.): '[p. 290] ... les branches du forceps sont vigoureusement appliquées par leurs extré – [p. 291] mités sur les parties latérales du VII^e sternite de la femelle (c'est-à-dire le dernier visible en surface).'. This led Richards (1927*b*: 262) to conclude that '... the stipes, volsella and squama, that is the most complex part of the genitalia, do not enter the abdomen of the female at all ...'. In contrast to this, present evidence confirms that for bumble bees the apices of the volsellae and gonostyli (= squamae) do grip tightly around the female sting base in the manner shown for *B. (Melanobombus) lapidarius* (see Kopelke, 1982: figs 1–3;

Williams, 1985: fig. 5), even among apparently rather divergent species (e.g. from direct examination of live paired *B. (Bombus) lucorum*, *B. (Sibiricobombus) asiaticus*, *B. (Melanobombus) rufofasciatus* and from a freshly-killed pair of *B. (Fervidobombus) niger* Franklin [= *B. atratus* Franklin, a name preoccupied by *B. mucidus* var. *atratus* Friese]). In fact, whether these claspers grip sternum VI or the sting base has little effect on the substance of Richards's arguments against the lock-and-key hypothesis, namely that the supposed 'lock' structures of the females are relatively undifferentiated among species and that inter-specific pairing is probably rarely attempted in any case. Eberhard (1985) believed that similar comments by Richards (1927*a*) showed that the male genitalia of bumble bees could not function as 'holdfast devices', although I have seen two pairs in museum collections that were still locked together firmly by their genitalia.

Eberhard (1985) suggested that an alternative explanation for the elaborate structure of male genitalia is that they function as female stimulaters, which have diverged as a result of inter-sexual selection by female choice. Of course this idea does not depend on an absence of the holdfast function, but it does require that a female should be able to discern differences in stimulation by males with subtly different genital morphology. However, at present there is little evidence from bumble bees either for the existence of the sensilla that would be required in those heavily sclerotised areas of the sting base that are clasped by the males, or for the definite rejection of some males in preference to others by females.

Another likely evolutionary explanation of the great range of morphology of the male genitalia of bumble bees is that they function primarily as impregnable holdfast devices, which have diverged as a result of intra-sexual competitive selection among males (Richards, 1927*a*; Williams, 1985). In Kashmir, male bumble bees were seen to attempt to catch and mount the females in order to clasp them with their genitalia, without any obvious courtship (for further details see the comments on mate-searching behaviour of male bumble bees in Kashmir). Any radical changes in the functional characters of the male clasping mechanism might only be inherited in the unlikely event that they appeared at the same time as the necessary reciprocal changes in the anatomy of the female. Consequently characters of the male claspers might be more conservative than characters that do not have to fit the female securely in order to prevent any interruption of copulation. Yet the competition from other males of the same species to dislodge a paired male for access to the same female might still favour any slight elaborations of structure if this would increase that male's chances of hanging on to reproduce. Competition among males can be intense (e.g. Free, 1971; Lloyd, 1981; pers. obs.), probably because a male bumble bee's principal influence on its reproductive success, other than through the quality of its ejaculate or possibly through the removal of competitor's sperm, is likely to be by maximising the number of matings that it can achieve. This may account in part for why bumble bee mating systems are usually variations of scramble competition polygyny (see the comments on male mate-searching behaviour).

Genera of Bombini

Many of the inferences of relationship among bumble bees from the preliminary cladistic analysis of characters of the male genitalia remain very tentative (Williams, 1985), especially those for some of the most morphologically divergent species (e.g. the North American *B. nevadensis* Cresson, see the comments on the Kashmir species of *Mendacibombus*). Nevertheless, further evidence from characters of the females (Ito & Sakagami, 1985) and from enzyme mobilities under electrophoresis (Pamilo *et al.*, 1987) supports the conclusion that the socially parasitic or 'cuckoo' bumble bees (*Psithyrus*) constitute a monophyletic group. It also appeared from the results of the preliminary cladistic analysis that *Mendacibombus* could be the monophyletic sister-group to all other bumble bees. This group in turn appeared to consist of two monophyletic sister-groups, the social parasites (*Psithyrus*) and all remaining bumble bees. Consequently the use of three genera was recommended: *Mendacibombus, Psithyrus* and *Bombus*.

Now that it has been possible to examine the male genitalia of most of the described species, the present interpretation is that *Mendacibombus* is probably paraphyletic with respect to all other bumble bees (Fig. 5, *Psithyrus* + *Bombus* represented by *B. exil*, see the comments on the Kashmir species of *Mendacibombus* and *B. (Psithyrus) bohemicus*). So recognising *Mendacibombus* as a genus for these peculiar, high mountain bees is unsatisfactory because it is no longer well supported by evidence of monophyly. But then the traditional concept of the genus *Bombus* that includes *Mendacibombus* as a subgenus, but not *Psithyrus*, is also apparently paraphyletic and so recognisable only by phenetic similarity.

A pragmatic solution is to return to an emphasis of the more widely- shared characters and of the

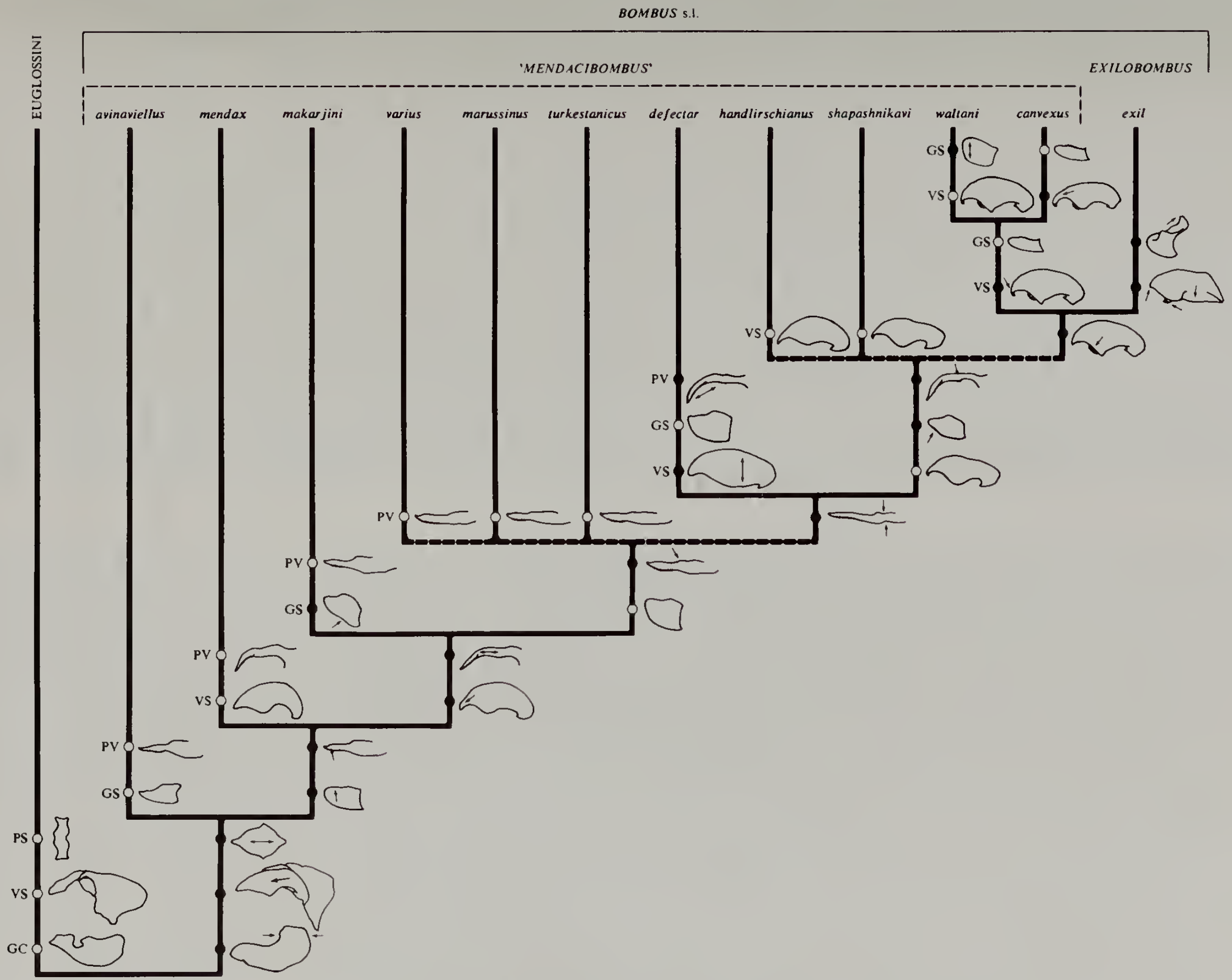


Fig. 5 Cladogram based on characters of the male genitalia for most species of the subgenus *Mendacibombus*, with *B. (Exilobombus) exil* representing all other bumble bees, including the species of *Psithyrus*. The name *varius* is a junior secondary homonym in the genus *Bombus* s.l. This taxon is likely to be conspecific with *B. himalayanus*, the males of which have not been examined (see the comments on *B. himalayanus*). Light circles show plesiomorphic states and dark circles show the appearance of apomorphic states. Character changes are shown by arrows (see Figs 44 & 45): PS, spatha of penis from the dorsal aspect; PV, right penis valve from the outer lateral aspect or dorso-posterior aspect; GS, right gonostylus from the dorsal aspect; VS, right volsella from the ventral aspect; GC, right gonocoxite from the dorsal aspect.

more distant affinities for the generic concept, with the result that one genus, *Bombus*, is recognised for all bumble bees, including *Psithyrus*. Of course the use of *Bombus* for all of these species does bring certain names originally ascribed to the genus *Psithyrus* into secondary homonymy with names in the genus *Bombus*. It also requires that qualifications concerning the socially parasitic species will have to be made more often to any generalisations about the species of *Bombus*. But despite this break with the most widely-established bi-generic tradition, the use of one genus for all bumble bees has the advantage that it recognises a group for which the evidence of monophyly is particularly strong, so that the nomenclature is most likely to remain stable. This single genus is also very easy for non-specialists to recognise.

Within the genus *Bombus*, the established subgeneric names (e.g. Richards, 1968) may be found convenient by some specialists who wish to label those assemblages of species that are more closely similar to one another. Unfortunately, Richards's usage of subgeneric names does not always communicate ideas of relationship well, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*) or even polyphyletic (e.g. *Sibiricobombus*, see the comments on *B. asiaticus* and *B. oberti*). Of course subgeneric names can simply be treated as synonyms of *Bombus* Latreille and ignored by those who prefer to do so. But when a comprehensive cladistic revision is available, then perhaps the nomenclature of the more reliably monophyletic species-groups could be revised, if the system is still found to be useful.

In this review, the bumble bee species of Kashmir are listed in a sequence that is chosen to reflect their relationships (after the sequencing convention of Nelson, 1972) as these are currently envisaged.

DISCRIMINATION OF SPECIES AND INTRASPECIFIC VARIATION

Early work on the taxonomy of Asian bumble bees showed little consistency in the delimitation of the taxa named as 'species' in some species-groups. In part this has been due to the changing nature of the species category as applied to living organisms. The species concept adopted for this review is briefly summarised here so that it is explicit.

A particularly visible part of the problem of discriminating species of bumble bees is that some of their populations are now known to include individuals with very different colour patterns. This was not always appreciated when only small samples were available from widely-scattered localities. Conspicuous colour patterns are likely to be advantageous because they advertise a warning to potential predators against the painful sting that female bumble bees can inflict. Consequently, the theory of Müllerian mimicry may explain not only the regional convergences in colour pattern among unrelated species, but also how parts of the same species may have diverged in colour pattern in different regions of its distribution (see the comments on characters not related to male mate-searching and the discussion of the colour patterns of the Kashmir fauna). It is perhaps precisely because bumble bees are such large and colourful insects that, like butterflies, they have been widely collected and have received so much attention in the literature. The considerable effort that has been invested in the description of subtleties of colour variation among some bumble bees has left an unfortunate nomenclatural burden of over 3000 formal names (i.e. about 12 names per species).

A large part of the more general problem in the application of the category 'species' to living organisms arises from confusion of the different kinds and degrees of relationship among populations (reviewed by e.g. Queiroz & Donoghue, 1988). Sexually reproducing organisms have been envisaged as living in populations that are united by interbreeding, so that in the long term relationships within the population tend to be reticulate. This provides the possibility of some evolutionary cohesion through gene flow, even though without concerted contraction and expansion of populations, random 'diffusion' of genes may not be sufficient to curb divergence (Barton, 1988). In contrast, relationships among populations are envisaged as tending to be more consistently divergent. In the short term, parts of a population may show restricted interbreeding with neighbouring parts of the population and may even show genetic and apomorphic divergence from them. Only with the benefit of hindsight is it possible to know whether divergence will be maintained or whether it will subsequently be dissipated in the broader population, should interbreeding become reinstated when the parts of the population meet. At one extreme, each of these parts of a population that may be more or less reproductively distinct in the short term could be regarded as a terminal element and given a name. But it can be seen that there is a broad range of possible relationships among these parts of the population, which may involve various degrees of inter-breeding both past and present, in differing combinations with various degrees of genetic and apomorphic divergence. Consequently, no absolute criterion can be devised that can universally define the species category.

Faced with the apparent impossibility of finding a universal solution to the 'species problem', it is still clearly desirable to try to minimise the confusion in the application of the species category. For the practice of discriminating species in this review, I have attempted to explore the application of species-defining criteria that place a greater emphasis on the potential for interbreeding (see the following section) than on general apomorphic divergence. General apomorphic divergence may have the appeal that it can be considered to have resulted in an observable pattern of monophyletic taxa, the discovery of which may be independent of any ideas of the process that caused it, which may not be discoverable. However, this rejection of process robs the 'morpho-species' category of any particular theory-based significance and so allows it to be defined only by a choice of some degree of apomorphic divergence that, in consequence, must be essentially arbitrary. Hence the cladistic method is not appropriate for the discovery of biological species. In contrast, the interbreeding criterion should be most closely associated with the process of gene flow within populations over the long term, which is believed to be one of the processes that can maintain some evolutionary cohesion (see Templeton, 1989). Of course there are also considerable problems with applying the interbreeding criterion, which are discussed in the next section. In practice, the application of the interbreeding criterion to many cases requires a similar degree of subjective judgement to that required by the use of the general apomorphic divergence criterion. Often the only available evidence for interbreeding is very indirect and must still be inferred from patterns of variation in characters of morphology or of molecules.

The 'biological' species and the Recognition Concept

Early authors may have regarded species as convenient classes for the typological description of a particular level of variation, but since Darwin (1859), the evolutionary significance of biological species has been stressed. This biological concept defines species of sexually reproducing organisms by a lack of interbreeding between populations, where these overlap. One of the problems with the biological species concept is that it does not solve the problem of interpretation for populations that do not overlap at present (reviewed by e.g. Splitter, 1982), because in its simple form it does not show how to obtain direct and representative evidence of the 'potential' for interbreeding between individuals that do not meet under natural conditions.

Dobzhansky (1937) suggested that isolating mechanisms have been selected for because they perform the function of preventing interbreeding between species. Isolating mechanisms were said to have the advantage of protecting their 'more harmonious' gene assemblages from disruptive recombination. But since isolating mechanisms might be selected for only when populations with such gene assemblages overlap, Dobzhansky's Isolation Concept provides little help in the assessment of the potential for interbreeding among non-overlapping (allopatric) populations.

Paterson (1980, 1985) criticised Dobzhansky's Isolation Concept of the species in response to difficulties with the population genetics of the selection of isolating mechanisms. Paterson's Recognition Concept defines a species by the common 'specific-mate recognition systems' that are shared by individuals in the population. From this viewpoint, individuals of different species are not expected to interbreed because they do not recognise one another as potential mates (thus 'postmating isolating mechanisms' [Mayr, 1963] are, strictly speaking, incidental to delimiting species). Paterson stressed that the breakdown in recognition at speciation might occur in allopatric populations, but only indirectly, as a consequence of other evolutionary divergences and not by reinforcement of hybrid disadvantage (i.e. 'premating isolating mechanisms' [Mayr, 1963] evolved as effects, and were not selected *for* their isolating function). Evidence of this particular kind of divergence in allopatry might help in the assessment of the potential for interbreeding among non-overlapping populations.

Paterson's Recognition Concept is not entirely satisfactory in that any allopatric populations with effective postmating isolation but no premating isolation would apparently be included in the same species. If these populations subsequently made contact, there would then be a selective advantage for reinforcement by premating isolation, as envisaged in the Isolation Concept.

Ultimately it is likely that both kinds of speciation process have occurred, so that a major contribution of the Recognition Concept may be its emphasis on the role of premating barriers or specific-mate recognition systems. Changes in these specific-mate recognition systems could evolve rapidly by sexual selection (see West-Eberhard, 1983) in allopatry, despite stabilising selection. Furthermore, neither stabilising selection nor sexual selection necessarily imply uniform selection pressures across a geographically extensive population and so they do not preclude the possibility of clinal variation in the recognition system (see Verrell, 1988). But if the characters that are crucial to specific-mate recognition were known to differ among individuals of at least some of the problematic disjunct populations, then the Recognition Concept might provide better grounds for discounting a potential for interbreeding and gene flow in these cases (e.g. Vrba, 1985).

In principle, the most widely-applicable morphological criterion for the discrimination of species might therefore be found where there are differences in the characters that function in specific-mate recognition. However, the Recognition Concept of species does not require individuals of separate species necessarily to differ at all in morphology (or in ecology, see Hengeveld, 1988) and the search for key characters for the discrimination of species has indeed been unsuccessful (reviewed by Templeton, 1981). This search can be traced to the classical concept of species as typological classes, whose members should share some particular similarity or 'essence'. More recently species have been viewed as individuals (Ghiselin, 1975), characterised instead by their internal organisation, within the population (Hull, 1980). This organisation could be provided by their shared specific-mate recognition systems and potential for interbreeding. Yet from a cladistic viewpoint, free interbreeding within a population is a shared ancestral characteristic and so does not define a taxon (Rosen, 1979). Cladists would therefore be obliged to recognise some paraphyletic terminal elements, because interbreeding populations are not always distinguished by the possession of convenient apomorphies by all individuals (e.g. Ackery & Vane-Wright, 1984; Queiroz & Donoghue, 1988). If apomorphic characters were always to become fixed throughout a population as a necessary part of the process of speciation, then these character states might fulfil the role of an essence. In contrast, character states correlated with specific-mate recognition systems are not essences because they may only be expected to evolve as secondary consequences of reproductive processes and they may occur in just one of the sexes. So these characters can provide no more than a guide for the inference of the potential for interbreeding among individuals as parts of the same species in certain cases.

Mate-searching behaviour of male bumble bees in Kashmir

The mate-searching behaviour of male bumble bees represents some of the first stages in the specific-mate recognition systems of these insects (cf. Paterson, 1985: fig. 2). In Kashmir, differences in male mate-searching behaviour among some closely-related species are associated with differences in some of their morphological character states, such as eye size and shape, antennal length and thoracic shape. Two contrasting examples are summarised briefly here (see the comments on the inference of allopatric, conspecific taxa & on allopatric, separate species). By analogy, these differences might provide a particularly strong form of morphological evidence from which to discriminate certain other likely species, even among preserved specimens in collections.

The use of characters related to specific-mate recognition systems for discriminating species still requires support from the study of the subsequent stages in the operation of these systems. Key components in this may involve certain volatile or contact pheromones. The head-gland secretions of males of European 'patrolling' species are believed to act as female arrestants (Svensson, 1979) and some of these secretions have been characterised (e.g. Bergström *et al.*, 1981). This has not been undertaken for female head-gland secretions, which may be just as important in the subsequent stage of specific-mate recognition by males (see Free, 1971; van Honk *et al.*, 1978). Some method to assay for behavioural discrimination between secretions of different composition by the organisms themselves in the field is now needed.

In 1985 I recorded the distribution of mate-searching activity in time and space from transect counts of numbers of male bumble bees around Gulmarg. Distribution with respect to altitude is described from altitudinal transects of the Pir Panjal range (the mountains on which Gulmarg is situated), between Tangmarg at 1800 m in the Vale of Kashmir, and the peak of Mt Apharwat above at 4143 m (13,592 ft) (total number of bumble bees identified > 2000, see Fig. 6). The habitat is described in more detail, together with the altitudinal distribution of foraging females, in the discussion of distribution with altitude. Spatial and temporal pattern in the distributions of mate-searching males can also be described at the smaller scale of a 30 m-high hill at Gulmarg, from vertical and horizontal transects (Figs 7 & 8).

I also recorded the activities of males that had

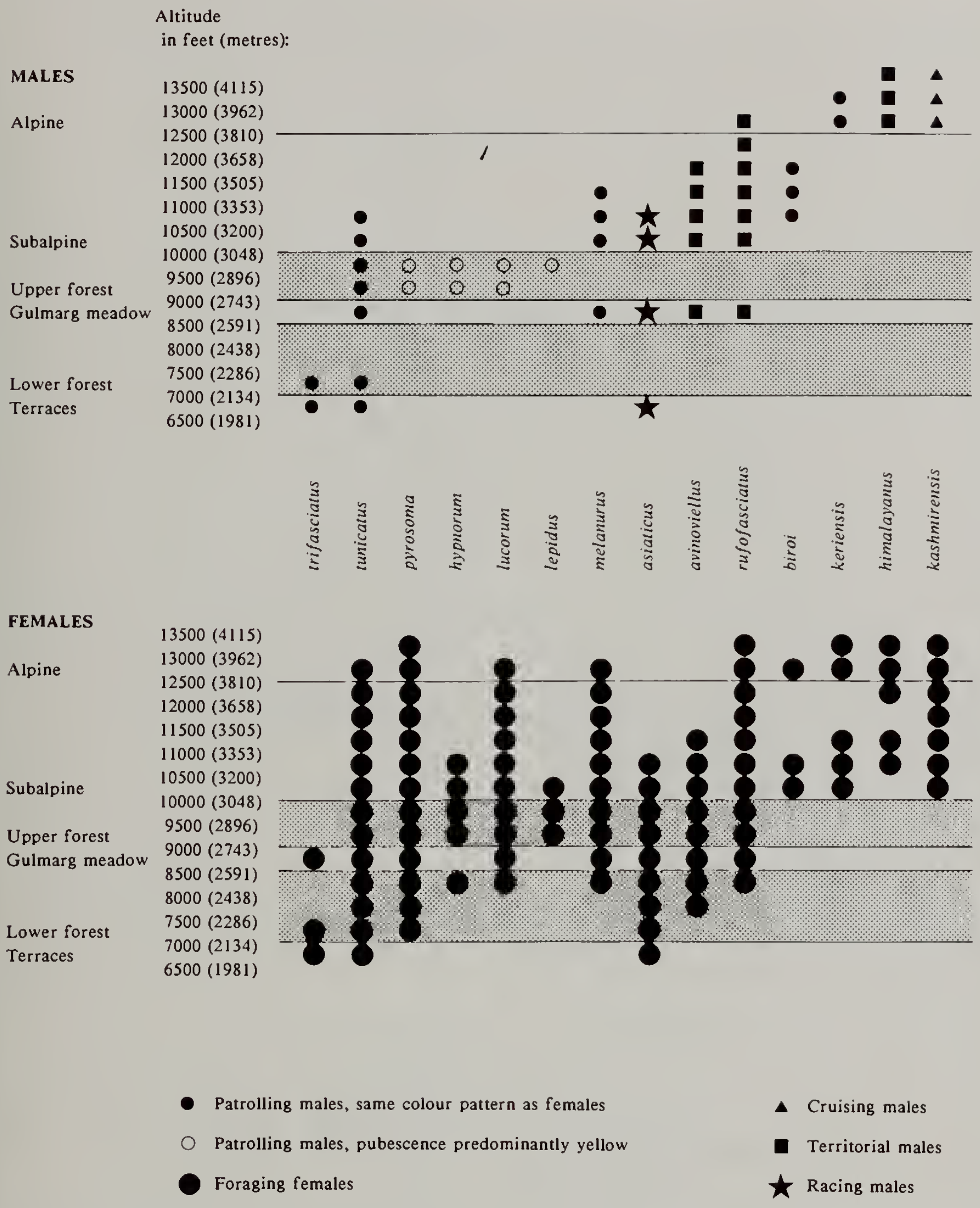
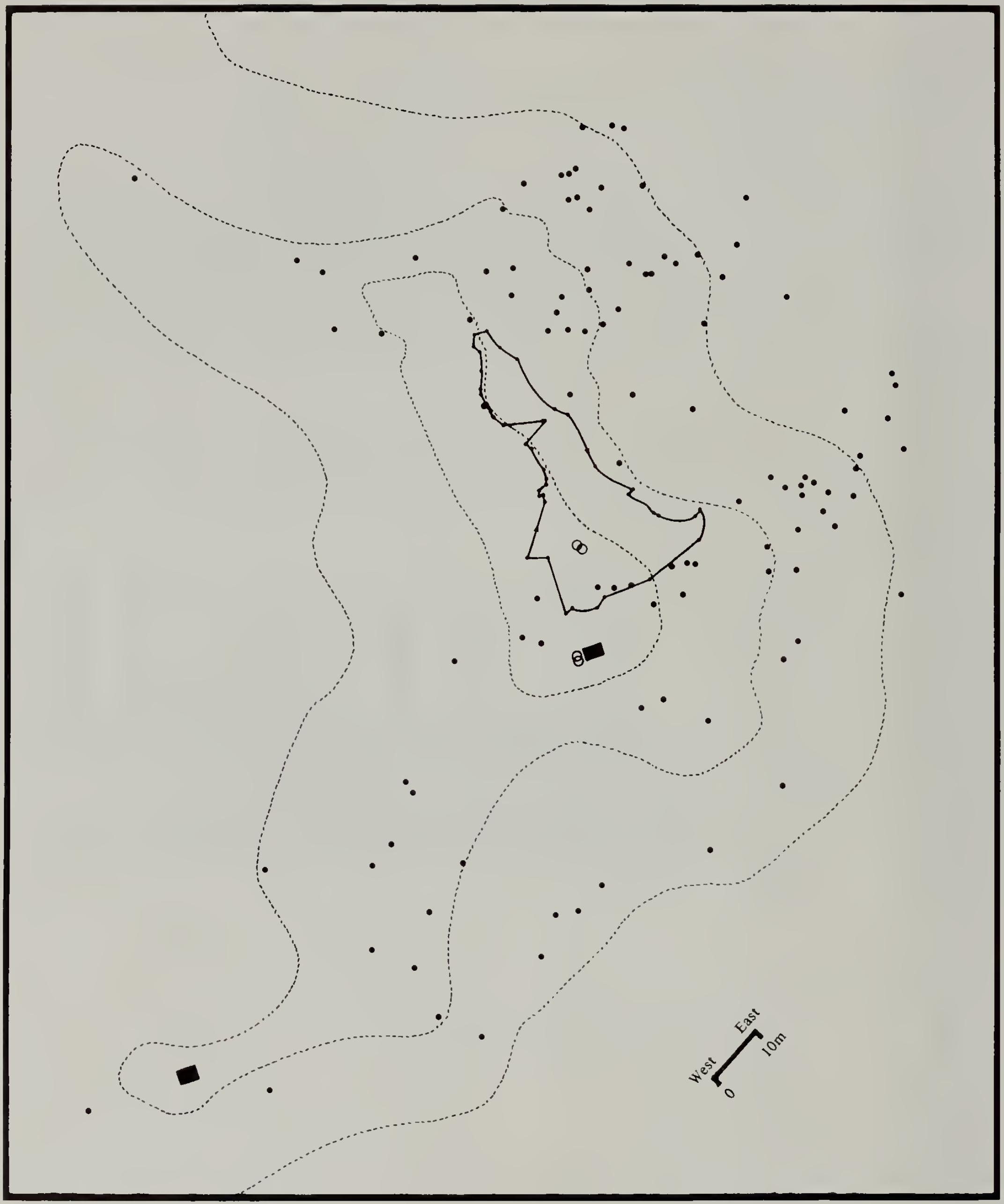


Fig. 6 Distribution of mate-searching males (above) and foraging females (below) of the social bumble bees (i.e. excluding species of the subgenus *Psithyrus*) with altitude on Mt Apharwat in the Pir Panjal Range around Gulmarg. Altitudes are estimated from the 500 ft contours of the 1 : 63,360 British Survey of India Map (Oxford University Library). Records are combined from transects made during July, August and September 1985. For a description of the vegetation in each habitat zone, see the discussion of distribution of the fauna with altitude.

been individually labelled, using the plastic tags that were developed for use with queen honey bees (52 male bumble bees were labelled in the vicinity of the 30 m hill in 1985; 108 males labelled in the same area in 1986). Numbered tags are ideal for the many perching males, which can be approached for their tags to be read, but plain discs of different colours are all that can be seen on patrolling bees, which spend most of their time in rapid flight. Labelling individuals did not obviously affect them adversely. For instance, one *B. tunicatus* male had resumed patrolling within 10 minutes of being released. Activities of males were recorded in part to compare their time



⁘ Perches of **racing** *B. asiaticus* males (29.viii.1986).

ꝏ Contested perch area of two **territorial** *B. rufofasciatus* males (20.viii.1985).

□ Circuit of places approached by a **patrolling** *B. tunicatus* male (14.viii.1985).

Fig. 7 Sketch map of the 30 m hill on Gulmarg meadow, showing the distribution of mate-searching activity by individually-labelled males of three species of bumble bees. Dotted lines show contours at 10 m intervals, black rectangles show the positions of two huts.

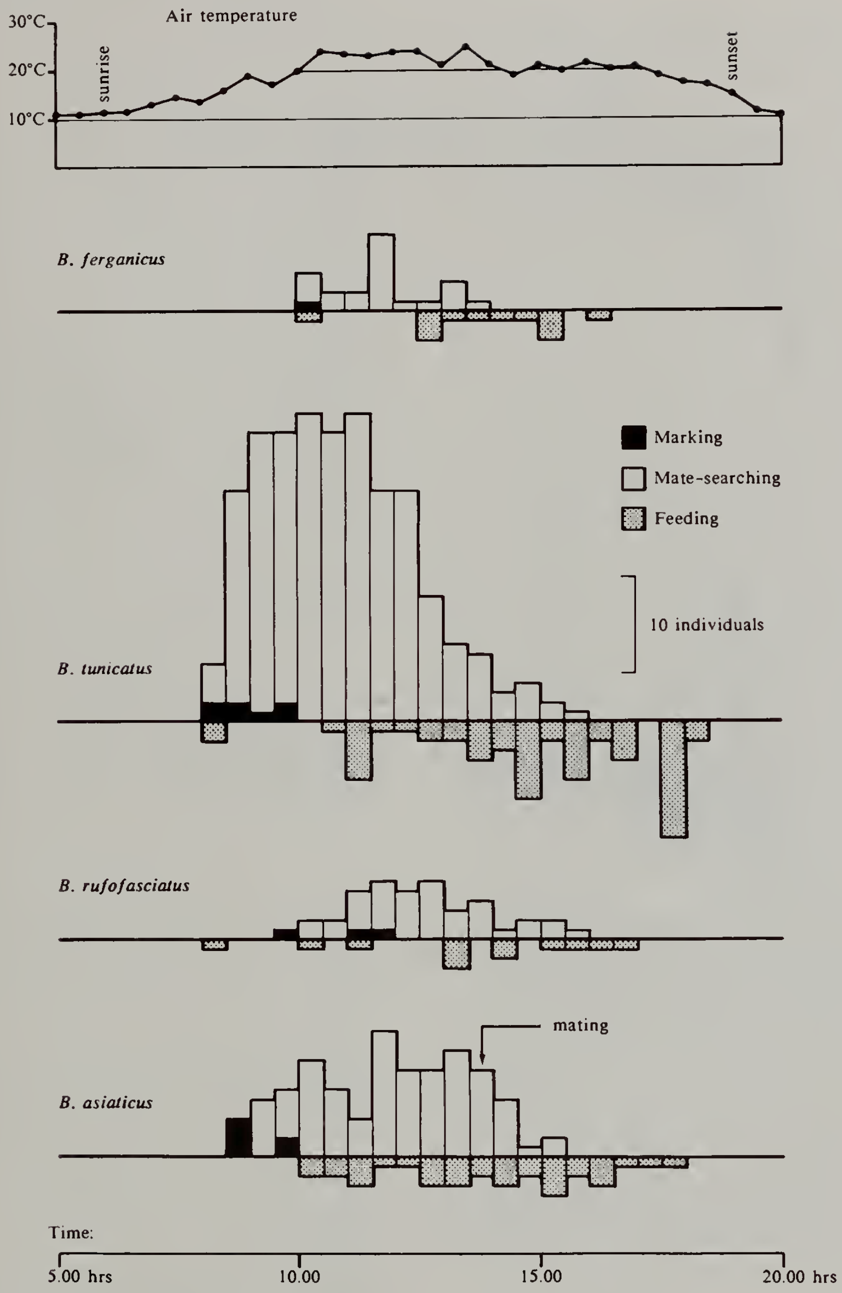


Fig. 8 Distribution of activity by males of four species of bumble bees between dawn and dusk on the 30 m hill in Gulmarg meadow. Counts were made every 30 mins during 19.viii.1985, along a transect of 450 paces around the 30 m contour at the top of the hill (see Fig. 7).

budgets, but also to record the nature and outcome of interactions between males. This included mapping the circuits followed on the 30 m hill by males of each of three species (*B. ferganicus*, *B. melanurus* and *B. tunicatus*), and mapping the perch positions of other species (*B. avinoviellus*, *B. rufofasciatus* and *B. asiaticus*). The reactions of males of all species to moving objects of different sizes were observed and tested. Young queens of *B. asiaticus* were tethered with lengths of thin black cotton at different places on the 30 m hill and the reactions of perching males were noted.

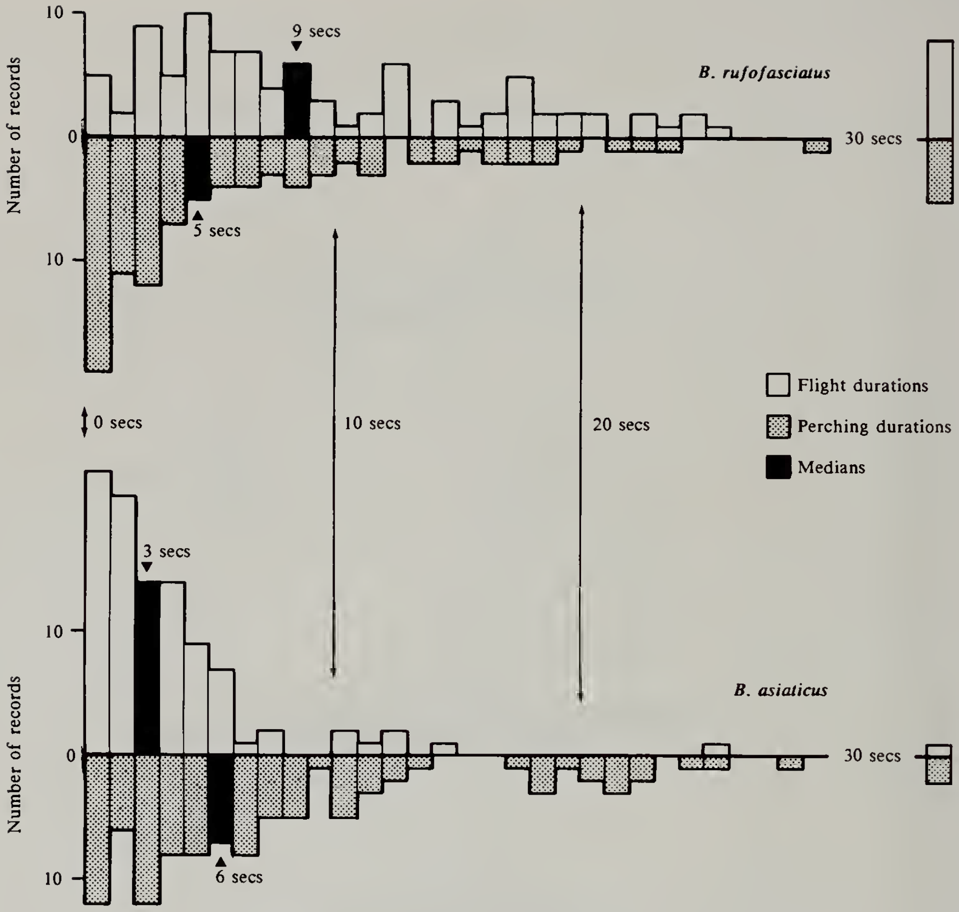


Fig. 9 Duration of consecutive flight and perching periods for mate-searching males of *B. rufofasciatus* (above) and *B. asiaticus* (below). For each species, records of 20 consecutive flight and perching periods were made from each of five males on the 30 m hill in Gulmarg meadow, during 11–12.viii.1985.

Four kinds of male mate-searching behaviour were observed during 1985. These are referred to here as 'patrolling', 'racing', true 'territorial' and 'cruising'. The territorial behaviour can be considered as an example of what has been termed pure dominance or lek polygyny, whereas the other three categories of behaviour represent divergent forms of scramble competition polygyny (see Thornhill & Alcock, 1983).

(A) **PATROLLING** behaviour has been described previously from British bumble bees and from most other European species (e.g. Darwin, see Freeman, 1968; Awram, 1970; Schremmer, 1972; Alford, 1975; Svensson, 1979). These males appear to mark objects early each day with an oral secretion, which presumably contains a pheromone. The objects are numerous, spaced by any distance from a few centimetres to some tens of metres, and chosen so that they can be patrolled as 'approached places' on a circuit flown regularly by the male. It has been suggested that receptive females are arrested at these pheromone 'traps' and that mating takes place when the male returns on his next patrol of the circuit (see Svensson, 1979). Examples of species whose males perform patrolling behaviour in Kashmir are *B. pyrosoma* and *B. tunicatus* (e.g. records from the 30 m hill, see Fig. 7). These males did not interact with one another directly nor did they respond to moving objects by pursuit, either near or between approached places.

(B) **RACING** behaviour differs from patrolling in that each male perches in one small area and will then pursue potential mates from this look-out position, but without competing with other males for preferred perches.

Racing behaviour is described here from *B. asiaticus*. These males perched on rocks, cowpats, leaves or fragments of wood (a maximum of 107 males were recorded at their perches on the 30 m hill on any one day, 29.viii.1986, Fig. 7). The perches were not associated with flowers (i.e. food resources) or nests (no nests of any species were found on the 30 m hill in either 1985 or 1986). Males would leave their perches in darting flights in pursuit of rapidly moving objects, which included conspecific queens and other males in flight, birds flying overhead and even stones thrown past the perch. Males rarely performed any slow inspection flights around perches (as shown by the short durations of flights by *B. asiaticus* males in Fig. 9). Successful pursuit flights with conspecific queens ended with the male bringing the queen to the ground, where he grappled with her, and attempted to mount her and clasp her sting base with his genitalia. There was no obvious courtship. When a queen was tethered, males approached rapidly and hovered for a few seconds, antennae almost in contact, before attempting to clasp her. Once a male had succeeded in clasping an untethered queen with his genitalia, she ceased pushing at him with her legs and the pair immediately flew from the area in tandem.

When a pursuit flight with a conspecific male resulted in an approach within a few centimetres, they diverged without clashing and returned to their perches without displacement of either male. Males were rarely found to have damaged limbs (2/108 labelled males, 1986, 30 m hill). Individual males returned to the same perches on many days (the maximum period spanned 27 days, 2–29.viii. 1986, male red-83, 30 m hill) and other males rarely usurped these perches after they had become vacant (occupancy is known to have changed for 5/170 perches 2.viii–11.ix.1986, 30 m hill, though only 108 males were individually labelled). Marking of perches with oral secretions was observed only occasionally, and only immediately after males arrived at their perches in the morning.

Some of these males were found to spend the night torpid in tight clusters of up to 10 individuals, deep among the short plant stems and roots on the middle slopes of the 30 m hill. Some individuals (e.g. male red-18, 1986) switched between clusters on successive nights, although this could have been the result of disturbance.

(C) **TERRITORIAL** behaviour differs from patrolling in that each male perches in one small area and will then pursue potential mates from this look-out position, but unlike racing behaviour, the males do compete for preferred perches.

Territorial behaviour is described here from *B. rufofasciatus* (e.g. on the 30 m hill, see Fig. 7). These males perched and pursued moving objects much as racing males did, but they also responded to conspecific males on their perches as well as in the air, and clashed audibly with them during extended chasing flights (Fig. 9). This may have contributed to the higher incidence of damage to appendages among these males (5/20 males labelled on the 30 m hill, 1985, had lost at least half of one antenna or leg) and did result in displacement from perches. For instance, on 18.viii.1985 male green-7 was perched above the entrance to a 3 m-long, 1 m-deep gully at the edge of the flat-topped 30 m hill. It left this perch to engage yellow-7 as it entered the gully, but after the ensuing chase, only yellow-7 returned to the gully, where it then perched within 10 cm of where green-7 had been. Later the same day green-7 returned, chased and replaced yellow-7 in this gully (occupancy changed at least 14 times for 9 perches 9–20.viii.1985, with or without contest, and 10 of these changes were for this gully). Yellow-7 then moved to a less frequently occupied perch area that was 10 m away on the side of the hill. These perches were not associated with nests or with concentrations of resources, but nevertheless continued to be highly preferred despite a high turnover in individual males (only 9 perch areas, each 2–4 m in diameter, could be found on the entire 30 m hill, but 20 males were labelled in these areas between 9–20.viii.1985). Males of *B. rufofasciatus* marked their perches with oral secretions much more frequently than did males of *B. asiaticus*.

The frequent inspection tours of *B. rufofasciatus* males around perch areas, such as the gully at the top of the 30 m hill, have a characteristic slow, stalling flight, with a low, interrupted buzz. Pursuit flights, like those of *B. asiaticus*, are much faster than the flight of females and have a higher-pitched buzz.

(D) **CRUISING** behaviour differs from patrolling in that each male uses one small area as a look-out position from which to pursue potential mates. Unlike racing behaviour, the males hover almost stationary in the air rather than perch, and unlike territorial behaviour the males do not compete for preferred positions.

Cruising behaviour was not seen on the 30 m hill and is described from observations of *B. kashmirensis* from just a few days (most on 23.viii.1985) near the peak of Mt Apharwat. These males maintained a very slow, almost hovering flight about 1 m above the ground, but each was confined within an area only 3–4 m across. From these aerial positions they pursued moving objects, much as racing and territorial

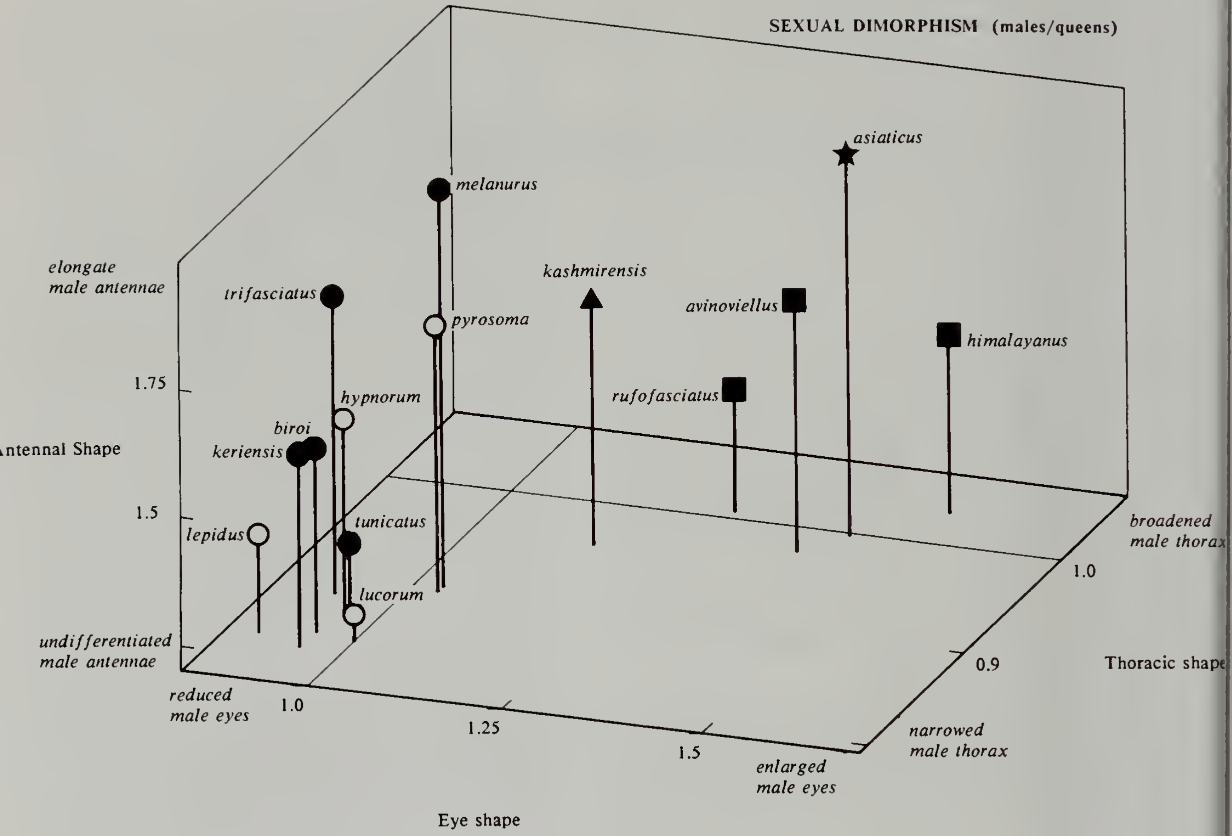


Fig. 10 Sexual dimorphism in some characters that may be related to male mate-searching behaviour among the social species of bumble bees (i.e. excluding species of the subgenus *Psithyrus*) of Mt Apharwat in the Pir Panjal Range. Shape dimorphism is measured as the ratio of mean shape of males/mean shape of queens, so values of 1.0 show no dimorphism in shape between males and queens. Eye shape is measured as the ratio of the maximum right compound eye length/minimum dorsal inter-compound eye distance; antennal shape is measured as right flagellum length/right scape length; and thoracic shape is measured as distance between and including tegulae/right radial cell length. Sample sizes (males/queens): *B. avinoviellus* (10/10), *B. himalayanus* (10/3), *B. trifasciatus* (8/5), *B. melanurus* (10/10), *B. kashmirensis* (10/10), *B. hypnorum* (10/4), *B. lepidus* (2/6), *B. biroi* (6/5), *B. tunicatus* (10/10), *B. lucorum* (8/3), *B. asiaticus* (10/10), *B. keriensis* (4/8), *B. pyrosoma* (10/10), *B. rufofasciatus* (10/10). Symbols show the different kinds of male mate-searching behaviour and colour pattern dimorphism (see Fig. 6, strong divergence in male colour pattern from worker colour pattern is only apparent among patrolling species): filled circles – patrolling males with similar colour pattern to females; open circles – patrolling males with pubescence predominantly yellow; star – racing males; squares – territorial males; triangle – cruising males.

males did on the 30 m hill. Cruising males also interacted in flight, but no clashes with violent physical contact were detected, no males were found to have damaged limbs (0/12 of the males collected) and no displacement of males was seen. Marking of vegetation with oral secretions within the cruised area was seen.

Patrolling behaviour is well known for bumble bees, but the other three categories are distinguished here for the first time. Males of a few species from central Europe and from North America have also been seen to return to perches between intermittent pursuit flights (e.g. Schremmer, 1972; Haas, 1976; Alcock & Alcock, 1983). Pairs of males of some of these species were seen to engage in protracted interactions, at least occasionally, so their behaviour may correspond to the territorial behaviour described here (e.g. Schremmer, 1972; Alcock & Alcock, 1983).

Sexual dimorphism in relative eye size, antennal length, wing shape and thorax shape is least strongly developed in patrolling ('marathon') species and more pronounced among the other 'perch and sprint' categories (e.g. review by Schremmer, 1972), especially for the racing species (Fig. 10). The species that patrol exclusively in the upper forest show pronounced sexual dimorphism in colour with similar, almost uniformly bright yellow males (see the discussion of colour patterns of the Kashmir fauna).

Relationship between male mate-searching behaviour and habitat structure

It seemed likely from a comparison of the male mate-searching behaviour among the bumble bees observed during 1985 that each of the four categories could have advantages for increasing a male's number of matings. But which of these kinds of behaviour is most advantageous to an individual male for maximising his mating success is likely to depend on the particular conditions of density and dispersion in the distributions of receptive females. This scheme is summarised in Table 2. Each species' characteristic density and dispersion of receptive females is expected to reflect the particular responses by its individuals to the different kinds of habitat in the mountains:

Table 2 Summary of the likely characteristics of the distributions of receptive female bumble bees on Mt Apharwat (altitudes 2700–4143 m), for the most abundant species in the four principal kinds of habitats (1985 survey). These different distributions may each favour one of the four groups of male mate-searching behaviour (in bold).

		Dispersion	
		high (even)	low (clumped)
Density	high	meadow **RACING** e.g. *B. asiaticus*	high alpine **CRUISING** e.g. *B. kashmirensis*
	low	forest **PATROLLING** e.g. *B. pyrosoma*	subalpine **TERRITORIAL** e.g. *B. rufofasciatus*

(A) **PATROLLING**. Males of all species found around Gulmarg to be mate-searching only within the forest (1900–3000 m) (e.g. *B. pyrosoma*), and males of the species most widespread among the different kinds of habitat (e.g. *B. tunicatus*), were patrolling in search of mates (Fig. 6). The densities of all bumble bees are expected to be especially low in the coniferous forest, where floral resources are scant (see the discussion of distribution with altitude). Dense forest has a complex physical structure, which reduces the visibility of potential mates and obscures any long range visual cues that might be used by individuals to aggregate for pairing. A web of pheromone traps, formed by the approached places that these males patrol, should be especially well suited for collecting mates at low, relatively uniform densities. Patrolling behaviour is also likely to work especially well in open habitats where young queens are present at low density and may not be predictably aggregated (e.g. arctic environments).

(B) **RACING**. Resources in the large meadow of Gulmarg are apparently much richer, because it appears to have the highest density of bumble bees among all of the areas surveyed on Mt Apharwat (see the discussion of distribution with altitude). For species specialising in this open habitat, patrolling behaviour might be expected to break down at high density if some males were to exploit the pheromone 'traps' at approached places by perching there and waiting for the more frequent females to arrive. At high density, males that persisted in patrolling would be wasting much of their time in flight between traps (when patrolling males may not be responsive to receptive females, see Free, 1971), without increasing their chances of finding a receptive female.

Racing *B. asiaticus* were present at more uniformly high densities than patrolling species, in some open, grassy areas below the forest (1800–1900 m), in parts of the meadow at Gulmarg (2650–2700 m) and just above the upper edge of the forest (3000–3100 m, Fig. 6). Males appeared to be less aggregated than those of the cruising or territorial species, which are associated with the higher relief, alpine habitats. This presumably reflects either a more even distribution of receptive females, or the unpredictable spatial pattern of this distribution in the meadow. Transect counts show a tendency for males to concentrate on steep ridges (vertical transects 16 & 23.viii. 1985: 53/86 males in steepest middle half of slope, 7.5–22.5 m up the 30 m hill; horizontal transect 18.viii.1985: 23/26 males on ridges rather than gullies) of south and east-facing slopes (i.e. facing the sun in the morning, see Fig. 7), but perch sites were still relatively widely and evenly spread. The mate-searching activities of *B. asiaticus* males were also spread over a longer period of weeks than those of the territorial or cruising species in subalpine and alpine habitats. This may reflect the longer season during which floral resources are available to fuel colony development and the rearing of young queens at the lower altitude of Gulmarg.

(C) **TERRITORIAL**. Above the forest, in the subalpine zone, the season of profitable foraging is shorter, the levels of resources may be lower than in the forest meadows, and so the bumble bee density is expected to be lower (see the discussion of distribution with altitude). The open subalpine zone covers a large area on Mt Apharwat, although it also provides abundant topological cues that could be exploited to facilitate the meeting of the sexes even if they are present at low density, for instance by local 'hilltopping' (hilltopping could arise through the evolution of female choice, see Kirkpatrick, 1982).

The most abundant species above the forest is *B. rufofasciatus*. Males were indeed seen to be very closely aggregated in small groups on the tops of shoulders protruding from the subalpine slopes of Apharwat (3000–3800 m) and, more rarely, in the alpine zone (c. 3900 m) and on top of the 30 m hill in the meadow at Gulmarg (2700 m, two perch areas shown in Fig. 7). At any one time these males were few in number, but were all closely associated with even fewer perch areas. So although perch areas were widely spaced, they each had up to seven males flying around them. If this does reflect the pattern in the distribution of receptive females, then territorial defence is likely to be more advantageous for these males than for species at higher densities, because it could win exclusive access to females at an especially attractive site, while the probability of missing a female during a male-male chase would be lower.

(D) **CRUISING**. Habitat conditions in the alpine zone resemble those in the subalpine, but are even more extreme in features such as the short foraging season (see the discussion of distribution with altitude). However, this open habitat has the ultimate topological cues for potential mates at low density to meet by hilltopping – the mountain peaks.

The most abundant high alpine specialist is *B. kashmirensis*. Workers forage throughout most of the alpine and subalpine zones (3000–4000 m, Fig. 6), but cruising males were found to be aggregated exclusively in the high alpine zone (4000–4100 m), in the lee of the peak of Mt Apharwat (4143 m). Moreover, males were seen on just a few of the days during which this area was visited, although in larger aggregations than the males of *B. rufofasciatus*, so that mate-searching activity may be highly concentrated in time as well as in space. Both factors could contribute greatly to enhance the encounter rate or effective local density of mates. If the female arrival rate were sufficiently high, then territorial chases between males might result in more females being missed, or lost to 'sneaky' males, than would be lost to tolerated competitors. The hovering flight of cruising males may be one way of gaining an advantage over perching competitors, both by saving time on take-off in pursuit of a potential mate and possibly by increasing the field of view. Thus it may be that, whereas racing males tolerate one another's proximity because no one perch site is predictably much more attractive to females than any other, a male cruising over a particularly attractive site tolerates the proximity of another male because displacing the competitor might cost more in lost opportunities than could be gained through attempts at sole possession.

The characteristics of density and dispersion in the distributions of receptive female bumble bees could not be measured directly. Young queens are not often seen before winter. More particularly, bumble bees have rarely been found *in copula*, despite their abundance. Preliminary searches had shown that male marking activity is greatest in the early morning, so I had expected that searching at this time might yield more observations of pairing. In fact this was seen only four times, all in the afternoon (e.g. Fig. 8). An explanation for the rarity with which bumble bees are seen paired, despite the length of time for which females remain clasped by the males (usually in excess of 20 minutes, pers. obs.), may lie with the observation that paired females and males flew in tandem from the areas where males were mate-searching as soon as the males had clasped the females, which took just a few seconds. This scattering to inconspicuous places may help to avoid competitive interference from other males of the same species. Unfortunately it also precludes the use of any observations of paired bumble bees as a measure of the distribution of receptive females.

Less direct methods may nonetheless reveal the distribution of receptive females. It can be assumed that it would be to the advantage of each individual male if the male were to invest its mate-searching efforts in time and space in a pattern that closely resembles the predictable component in the distribution of receptive females. Therefore the density and dispersion of mate-searching males should reflect the pattern for receptive females.

Estimates of density and dispersion of mate-searching males were made from transect counts in each of the principal habitats at Gulmarg during the summer of 1986 (Tables 3 & 4). Only 54 mate-searching males of *B. pyrosoma, B. asiaticus, B. rufofasciatus* and *B. kashmirensis* were recorded during this transect census. The spring thaw had been unusually late and the summer was cold and wet. The peak of mate-searching activity by males of the alpine and subalpine bumble bee species

Table 3 Estimates of mean/variance ratio in the number of mate-searching males among 160 m segments of transect on Mt Apharwat as a measure of male dispersion (12 & 14.ix.1986). The figures were calculated for each of the most abundant species only within its associated habitat (see Table 2).

Dispersion			
high (even)		low (clumped)	
B. asiaticus	0.51	*B. kashmirensis*	0.21
B. pyrosoma	0.61	*B. rufofasciatus*	0.14

Table 4 Estimates of mean number of mate-searching males counted along each 1 km of transect on Mt Apharwat as a measure of male density (12 & 14.ix.1986). The figures were calculated for each of the most abundant species only within its associated habitat (see Table 2).

Density	high	*B. asiaticus*	8.8	*B. kashmirensis*	4.4
	low	*B. pyrosoma*	3.1	*B. rufofasciatus*	1.7

was about 20 days later in 1986 than it had been in 1985 and their density also appeared to be lower in 1986 (e.g. males of *B. rufofasciatus* were found on the 30 m hill at Gulmarg during 1985 but not during 1986). Further counts were prevented by the first heavy fall of snow, which blanketed the subalpine and alpine zones the morning after the first complete transect census.

Despite the small size of the sample in 1986, the figures in Tables 3 & 4 do appear to corroborate the expected characteristics of the common bumble bee distributions as postulated in Table 2, at least insofar as the figures in adjacent cells of the tables differ in the expected directions. Of course this result is only an apparent correlation based on observations of the bumble bees on one mountain and does not constitute a test of the relationship.

The behaviour of one group of *B. rufofasciatus* males on a high, steep-sided shoulder of Mt Apharwat (c. 3700 m, 23.viii.85) provides stronger support for the importance of distribution, although it is still only circumstantial evidence. In this situation their behaviour was apparently not territorial but resembled the cruising of *B. kashmirensis*. Conforming with the pattern in Table 2, these *B. rufofasciatus* males had formed a large group of unusually high density (estimated to be 50–100 males). However, it must be noted that individuals of most species are apparently not this flexible in their behaviour. For instance, *B. asiaticus* males were never found patrolling, even where they were present at low density. No males of patrolling species were found racing, either at localities with unusually high density or otherwise.

If differences in habitat structure between separated (allopatric, peripatric or parapatric) parts of an ancestral population may affect the balance of advantage among the different kinds of mate-searching behaviour, then the mate-searching behaviour of the descendent populations could diverge very rapidly by sexual selection. This may be particularly likely to affect the specific-mate recognition system and could result in speciation (see Rice, 1987, for a similar model for sympatric speciation).

Inference of allopatric, conspecific taxa

Several nominal taxa that are closely similar in morphology show pronounced variation in the colour pattern of the pubescence among adjacent regions. One example is provided by individuals with the two principal colour patterns that are ascribed to *B. asiaticus* in Kashmir (see the comments on *B. asiaticus*). Individuals with both the unbanded yellow pattern (e.g. Figs 371–376) and the banded grey-white pattern (e.g. Figs 386, 387, 389–391) of *B. asiaticus* occupy similar open meadow or steppe habitats on either side of the Great Himalaya range (Map 48). The mate-searching behaviour of the males in the two regions could not be distinguished and consists of the racing behaviour that is unique to these nominal taxa among the bumble bees of Kashmir. This close similarity in mate-searching behaviour is reflected in the similarity of the associated morphological characters of the males, such as their much larger eyes and longer antennae in relation to those of the females (Fig. 10). Supporting evidence for interbreeding between individuals with the different principal colour patterns is provided by specimens with intermediate colour patterns (Figs 377–382) from a few localities in high valleys of the Great Himalaya. The frequencies of the different states for two of the three variable colour characters examined from these localities is consistent with simple models of population genetics (see the discussion of variation of *B. asiaticus* in Kashmir). So as parts of what appears to be a single, interbreeding population, these nominal taxa are considered to be parts of a single species.

Inference of allopatric, separate species

Discontinuous geographical variation has also been found in the morphological characters that are associated with the different kinds of male mate-searching behaviour, between what are in other respects very similar nominal taxa. *B. wurflenii* is widespread in Europe among the upper forests of mountains, where the males, which patrol their scent-traps within the forests in search of mates (pers. obs., Austrian Alps), have eyes similar in size to those of the females. The morphologically similar *B. kashmirensis* is widespread in the Himalaya and eastern Tibet (Map 31) among the open alpine zones. The principal difference from *B. wurflenii* is that the males of *B. kashmirensis* possess slightly-enlarged eyes relative to the females (Fig. 10). On Mt Apharwat in Kashmir at least, these males apparently aggregate in the neighbourhood of mountain peaks, where they 'cruise' in search of females by sight. If this behaviour is representative and constant, then individuals of the two taxa would be unlikely to interbreed even if they were to occur on the same mountain, because they appear to search for mates in different ways and in different kinds of habitat. They may therefore have diverged in at least the first stages of their specific-mate recognition systems and so can be considered to be separate species (see the comments on *B. kashmirensis*, and on another group of more or less parapatric sister-species, *B. simillimus*, *B. pyrosoma* and *B. rufofasciatus*).

Characters of species not related to male mate-searching behaviour

Unfortunately the mate-searching behaviour component of the specific-mate recognition system only differs sufficiently among species for divergence in associated morphological characters to be apparent in a few cases. So, of necessity, discrimination of most species still depends on the interpretation of even less direct evidence of interbreeding. This is usually inferred from a diagnosis by a combination of other morphological characters. Specimens are now available from many more localities in Kashmir so that a more comprehensive examination of the variation in these characters among individuals can be made.

At the beginning of this study, cladistic methods were used to divide material in collections into what are likely to be monophyletic taxa by character state patterns of the male genitalia. Material was further sorted by sample sites. Patterns of variation in a broad range of characters were then examined for description, both within and among these groups of individuals.

For the discrimination of species, particular attention was paid to any strictly coincident discontinuities in the patterns of character variation among individuals, irrespective of whether they occur between the supposedly monophyletic taxa or within them. These coincident discontinuities may provide evidence for barriers to interbreeding between populations and so may show the presence of separate species, which need not correspond to monophyletic taxa.

On the other hand, where individuals were found that show intermediate or mixtures of character states between the otherwise differentiated taxa, this is interpreted as evidence in favour of the occurrence of hybridisation between them, as parts of a single population and a single species. For instance, in Europe wide variation is known to occur between parapatric parts of the population of *B. soroeensis* (Fabricius). Individuals of this species from much of Russia, Scandinavia, Britain and Spain are banded yellow bumble bees with white 'tails'. Individuals from central and south-eastern Europe are unbanded, red-'tailed' bees. But individuals from the intervening areas in both France and eastern Europe show a continuous range of variation in both characters between the two, more widespread, colour patterns (Reinig, 1939: fig. 10). In some areas, individuals with both principal colour patterns may even be reared from the same nest, apparently as the offspring of the same queen (Vogt, 1909). Therefore individuals with either of these two colour patterns have been considered to be interbreeding as parts of the more or less continuous population of a single species.

Zones of hybridisation between nominal taxa can be very narrow, with steep clines in character frequencies (see e.g. Mallet, 1986; Hewitt, 1988). For instance, localised steep clines in hybrid zones are well known for groups of colour pattern characters within populations of certain European bumble bees (e.g. Reinig, 1970). Yet as long as some evolutionary cohesion could be maintained by the passage of some alleles across a hybrid zone through interbreeding, then the parts of the population could be considered to be parts of a single species. Among Sino-Himalayan bumble bees, some of the most difficult decisions concerning conspecific status involve bees from the montane forests (e.g. see the comments on *B. lepidus*, *B. pyrosoma*). These forests are confined to a long, narrow ribbon around the southern and eastern edges of the great Tibetan massif. In this situation, any hybrid zones across this ribbon are likely to be much shorter than those described for *B. soroeensis* in Europe and so more difficult to locate and study adequately.

If some of the provisional decisions reached in this review in cases where the available information remains inconclusive seem unduly biassed in the direction of 'lumping', it is because the burden of proof of a divisive speciation event within an ancestral population is considered to rest with the 'splitter'. It has been argued that evidence from subtle differences between two individuals is not sufficient. For example, it can be seen that the people from the different parts of Europe, of Asia, or even from different areas within Kashmir, also vary in shape and hair colour, and yet from their breeding behaviour they would all be placed in one biological species.

But irrespective of the decisions reached here, as much of the available information as time has allowed is presented in the comments on the variation within Kashmir and in the figures and maps, so that readers with a different concept of the nature of species should be able to make their own decisions regarding this fauna.

The description of intraspecific variation

Many examples of character variation among samples of a single species can be related to where the samples were collected within the species' distribution. Often this geographic variation in single characters can be regarded as belonging to a continuum between extreme states, so that defining two or more discrete states would require threshold criteria that must be essentially arbitrary. Furthermore, where comparisons are drawn between two or more characters, these may show geographically incongruent patterns of variation, so that most combinations of states can be found somewhere within the species' distribution. Therefore, because variation of characters among individuals does not always delimit discrete sub-units within populations (Wilson & Brown, 1953; but see Mallet, 1986; Barton, 1988), previously described nominal taxa of subspecific rank are not attributed here with formal names. This removes any requirement for a general subspecies concept that would otherwise necessitate imposing more assumptions about the genetic structure of populations. The significance of intraspecific variation is better judged separately for the different cases that are presented by each species.

In the place of the earlier systems of subspecific and infrasubspecific nomenclature, in this review the most obvious character states are referred to using shorthand descriptions. An example is an 'unbanded (= no band of black pubescence between the wing bases) yellow (= colour of the pale pubescence, excluding any red hairs on the apical terga) queen (= large female) of *Bombus asiaticus*'. This terminology may appear less elegant, but it has the advantage that it is easily modified to give a more precise description of the recognised attributes of a particular individual.

Intraspecific variation of selected characters is described separately for each species as it is represented in the samples available, together with the frequencies of the various states in these samples. These frequencies may have been biassed at some sites by selective collecting, at least for the later samples (1985, 1986). But for the maps of the geographical distribution of variation in the bees' colour patterns, it is necessary for clarity of presentation to resort to a more typological approach, referring instead to the predominant local phenotype among the workers (see the figures accompanying the maps). This emphasis is placed on the workers because they are usually the most abundant sex and caste to be seen by collectors. Species' distributions within Kashmir are shown by spot maps rather than by grid maps, because sampling effort could not be even nearly uniform across the country (Map 4; see the comments on material examined and depositories).

NOMENCLATURAL SUMMARY

Where possible type specimens have been examined in order to assign specific nomenclature more precisely. References in the text to 'Art. n' allude to the numbered articles of the *International Code of Zoological Nomenclature* (ICZN, 1985).

Synonyms are listed here only in cases where I have examined the types or specifically discussed their identity. Names of taxa whose status as part of the same species is in particular doubt are cited as provisional synonyms. Unavailable names are cited in brackets. Nomenclatural details for taxa in the genus group are not repeated in this section.

BOMBUS Latreille 1802*a*
- ***avinoviellus*** (Skorikov, 1914*a*)
  - *callophenax* Cockerell, 1917 **syn. n.**
  - [*subtunicatus* Richards, 1930, infrasubspecific]
- ***himalayanus*** (Skorikov, 1914*a*)
  - *varius* (Skorikov, 1914*a*) (provisional synonym)
- ***marussinus*** Skorikov, 1910*a*
  - *afghanus* Reinig, 1940 **syn. n.**
- ***bohemicus*** Seidl, 1837
  - *nemorum* (Fabricius, 1775)
- ***novus*** (Frison, 1933) **comb. n.**
  - *nepalensis* (Tkalců, 1974*b*) (provisional synonym)
- ***branickii*** (Radoszkowski, 1893) **comb. n.**
  - *eriophoroides* (Reinig, 1930)
  - *elisabethae* (Reinig, 1940)
- ***ferganicus*** (Radoszkowski, 1893) **comb. n.**
  - *indicus* (Richards, 1929*a*)
- ***morawitzianus*** (Popov, 1931) **comb. n.**
  - *redikorzevi* (Popov, 1931)

- ***skorikovi*** (Popov, 1927*b*) **comb. n.**
  - [*mesoxanthus* (Richards, 1928*c*) infrasubspecific]
  - *gansuensis* (Popov, 1931)
- ***trifasciatus*** Smith, 1852*a*
  - *montivagus* Smith, 1878*b* **syn. n.**
  - *secundus* Dalla Torre, 1890 **syn. n.**
  - *ningpoensis* Friese, 1909
  - *wilemani* Cockerell, 1911 (provisional synonym)
  - *albopleuralis* Friese, 1916 **syn. n.**
  - *maxwelli* Pendlebury, 1923 (provisional synonym)
  - *mimeticus* Richards, 1931 **syn. n.**
  - *albolateralis* Richards, 1931 **syn. n.**
  - *gantokiensis* Richards, 1931 **syn. n.**
  - *turneri* Richards, 1931 **syn. n.**
  - *insidiosus* Richards, 1931 **syn. n.**
  - *geminatus* Richards, 1931 **syn. n.**
  - *magrettianus* Richards, 1931 **syn. n.**
  - *minshanicus* Bischoff, 1936 **syn. n.**
  - *quasibreviceps* (Tkalců, 1968*b*) **syn. n.**
  - *atropygus* (Tkalců, 1989) **syn. n.**
- ***haemorrhoidalis*** Smith, 1852*a*
  - *orientalis* Smith, 1854 **syn. n.**
  - *buccinatoris* Smith, 1879 **syn. n.**
  - *assamensis* Bingham, 1897 **syn. n.**
  - *montivolans* Richards, 1929*b* **syn. n.**
  - *khasianus* Richards, 1929*b* **syn. n.**
  - *semibreviceps* (Tkalců, 1968*b*) **syn. n.**
  - *semicoloricontrarius* (Tkalců, 1968*b*) **syn. n.**
  - *cinnameus* (Tkalců, 1989) **syn. n.**
- ***melanurus*** Lepeletier, 1836
  - *tschitscherini* Radoszkowski, 1862 **syn. n.**
  - *difficillimus* Skorikov, 1912*b* (provisional synonym)
  - *subdistinctus* Richards, 1928*b* **syn. n.**
  - *griseofasciatus* Reinig, 1930 (provisional synonym)
  - *maidli* Pittioni, 1939*b* **syn. n.**
- ***personatus*** Smith, 1879
  - *roborowskyi* Morawitz, 1886 **syn. n.**
- ***kashmirensis*** Friese, 1909
  - *stramineus* Friese, 1909
  - *tetrachromus* Cockerell, 1909
  - *pulcherrimus* (Skorikov, 1914*a*)
  - *meinertzhageni* Richards, 1928*b*
  - [*albohirtus* Richards, 1930, infrasubspecific]
  - *beresovskii* (Skorikov, 1933*b*) **syn. n.**
- ***hypnorum*** (Linnaeus, 1758)
  - *bryorum* Richards, 1930 **syn. n.**
  - *fletcheri* Richards, 1934 **syn. n.**
- ***subtypicus*** (Skorikov, 1914*c*) **comb. n.**
  - *leucopygus* Morawitz *in* Fedtschenko, 1875
  - *leucurus* Bischoff & Hedicke, 1931
  - *kohistanensis* (Tkalců, 1989) **syn. n.**
- ***lemniscatus*** Skorikov, 1912*b*
  - *flavopilosus* Friese, 1918 **syn. n.**
  - *peralpinus* Richards, 1930
- ***lepidus*** Skorikov, 1912*b*
  - *genitalis* Friese, 1913 **syn. n.**
  - *tetrachromus* Friese, 1918 **syn. n.**
  - *yuennanicola* Bischoff, 1936 (provisional synonym)
  - *hilaris* (Tkalců, 1989) **syn. n.**
- ***biroi*** Vogt, 1911
  - *flavobistriatus* Vogt, 1911 **syn. n.**
  - [*flavostriatus* Vogt, 1911, infrasubspecific]
  - [*flavofasciatus* Vogt, 1911, infrasubspecific]
  - *nursei* Friese, 1918 **syn. n.**
  - *abbotti* Cockerell, 1922
  - *agnatus* Skorikov, 1933*b* (provisional synonym)
  - *kotzschi* Reinig, 1940 (provisional synonym)
- ***tunicatus*** Smith, 1852*a*
  - *gilgitensis* Cockerell, 1905 **syn. n.**
  - *simlaensis* Friese, 1909
  - *fulvocinctus* Friese, 1909
- ***lucorum*** (Linnaeus, 1761)
  - *cryptarum* (Fabricius, 1775) (provisional synonym)
  - *modestus* Cresson, 1863
  - *moderatus* Cresson, 1863
  - *magnus* Vogt, 1911 (provisional synonym)
  - *jacobsoni* Skorikov, 1912*b* **syn. n.**
  - *lucocryptarum* Ball, 1914 (provisional synonym)
  - *longipennis* Friese, 1918 **syn. n.**
  - *alaiensis* Reinig, 1930 **syn. n.**
  - *mongolicus* Krüger, 1954 **syn. n.**
  - *reinigi* Tkalců, 1974*b* **syn. n.**
- ***asiaticus*** Morawitz *in* Fedtschenko, 1875
  - *longiceps* Smith, 1878*a*
  - *regeli* Morawitz, 1880
  - *miniatocaudatus* Vogt, 1911
  - [*fuscocaudatus* Vogt, 1911, infrasubspecific]
  - [*albocaudatus* Vogt, 1911, infrasubspecific]
  - [*tenuifasciatus* Vogt, 1911, infrasubspecific]
  - *falsificus* Richards, 1930 **syn. n.**
  - *flavodorsalis* (Skorikov, 1933*b*)
  - *oshanini* (Skorikov, 1933*b*)
- ***oberti*** Morawitz, 1883
  - *semenovi* Morawitz, 1886 **syn. n.**
  - *duanjiaoris* Wang, 1982 **syn. n.**
- ***ladakhensis*** Richards, 1928*b*
  - *phariensis* Richards, 1930 **syn. n.**
  - *variopictus* Skorikov, 1933*b* **syn. n.**
  - *bianchii* Skorikov, 1933*b*
  - *reticulatus* Bischoff, 1936 **syn. n.**
- ***semenovianus*** (Skorikov, 1914*a*)
  - *problematicus* Bischoff, 1935
- ***keriensis*** Morawitz, 1886
  - *separandus* Vogt, 1909 **syn. n.**
  - *kohli* Vogt, 1909 **syn. n.**
  - *postzonatus* Vogt, 1909 **syn. n.**
  - *kozlovi* Skorikov, 1910*b* **syn. n.**
  - *incertoides* Vogt, 1911 **syn. n.**
  - *tenellus* Friese, 1913 **syn. n.**
  - *meridialis* (Skorikov, 1914*a*) **syn. n.**
  - *alpivagus* Richards, 1930 **syn. n.**
  - *karakorumensis* (Tkalců, 1989) **syn. n.**
- ***simillimus*** Smith, 1852*b*
  - *grossiventris* Friese, 1931 **syn. n.**
  - *oculatus* (Frison, 1933) **syn. n.**
  - *tonsus* (Skorikov, 1933*b*) **syn. n.**
  - *haemorrhous* Richards, 1934 **syn. n.**
- ***pyrosoma*** Morawitz, 1890
  - *flavothoracicus* Bingham, 1897 (provisional synonym)
  - *miniatus* Bingham, 1897 (provisional synonym)

[*canosocollaris* Skorikov, 1912*b*, infrasubspecific]
friseanus Skorikov, 1933*a* **syn. n.**
formosellus (Frison, 1934) (provisional synonym)
hoenei Bischoff, 1936 **syn. n.**
[*flavocorbicularis* Tkalců, 1961, infrasubspecific]
wutaishanensis (Tkalců, 1968*a*) **syn. n.**
rufofasciatus Smith, 1852*b*
prshewalskyi Morawitz, 1880
rufocinctus Morawitz, 1880
chinensis Dalla Torre, 1890
championi Richards, 1928*a* **syn. n.**
[*rufior* Richards, 1928*b*, infrasubspecific]
[*intermedius* Richards, 1930, infrasubspecific]
waterstoni Richards, 1934

TAXONOMY OF THE KASHMIR BOMBINI

BOMBINI Michener

Bombini Michener, 1944: 290. Type genus: *Bombus* Latreille, 1802*a*: 437.

In this review, formal descriptions of bumble bees are not repeated because the literature already contains many descriptions of particular individuals. Instead I describe just a few characters that may be useful to distinguish species. Tentative interpretations of some of these character-state patterns are included for the continuing discussion of relationships among species.

In the keys, those characters that have been found more reliably diagnostic have generally been placed nearer the beginning of each couplet. Characters of the genitalia are used frequently in the key to males (see Figs 44 & 45), so male specimens should be prepared for examination by extraction of their genital capsules. Colour patterns of the pubescence are used in the final stages of the keys for the determination of species within a species-group, where the range of variation does not overlap among these species within Kashmir. But after a reference collection has been prepared for a particular locality using the keys, it may often be possible to identify the majority of further specimens accurately by direct comparison, using only selected details of their colour patterns. Diagrams of the colour patterns are provided here to illustrate some of the variation (Figs 232–439). These diagrams should be coloured by hand to render them more immediately intelligible (see Fig. 258 for a colour key). Inevitably these diagrams are a compromise between portraying the general appearance of an insect and accurately showing the position of every coloured hair. For instance, the presence of a minority of black hairs among pale pubescence could not be shown without reducing the general resemblance of the diagram to the insect. Consequently these diagrams provide only a guide that should not be used without the keys.

Records of food-plants are included from notes made in the field during 1980, 1985 and 1986. These plant species were identified by reference to Polunin & Stainton (1984). The lists are by no means exhaustive, but they do include at least some of the preferred species.

Key to species (females: queens and workers)

1 Outer surface of hind tibia flat or partially concave, without long hairs on posterior part of lower or distal half of outer surface (corbicula), but with a comb of stout spines (rastellum) along inner distal margin (Figs 225 & 226); gastral sternum VI without ventro-lateral keels; clypeus strongly protuberant, with lateral margins curved back towards occiput (Fig. 15) 2

– Outer surface of hind tibia convex, with moderate to long hairs throughout, but without a comb of stout spines along inner distal margin; gastral sternum VI with a pair of ventro-lateral keels (Figs 206–211); clypeus nearly uniformly flat, only apico-lateral corners curved back strongly towards occiput 5

2 Outer (corbicular) surface of hind tibia usually smooth and shining or only weakly sculptured (reticulate coriaceous), without any long stout hairs arising from posterior part of outer surface below upper or proximal quarter (Fig. 226); proximoposterior corner of hind basitarsus strongly and acutely produced, projection longer than its own basal breadth (Figs 41 & 42); labrum with basal transverse depression extending apically as a deep median furrow between pronounced lateral tubercles, displacing ridge between them to form a lamella that overhangs apical margin (Figs 25 & 26) 10

– Outer (corbicular) surface of hind tibia coarsely sculptured (imbricate), appearing very rough, with widely-spaced long stout hairs or bristles arising from near middle of outer surface throughout upper or proximal half (Fig. 225); proximo-posterior corner of hind basitarsus rounded, projection no longer than its own basal breadth (Fig. 43); labrum with a narrow transverse basal depression, leaving a straight transverse ridge joining weak lateral tubercles, so that there is no median furrow and no apical lamella (Figs 23, 220–222) 3

3 (Subgenus *Mendacibombus*.) Ridge between labral tubercles is, at its mid point, narrower than basal depression (Figs 23 & 220), with few punctures and shining; wings clouded with brown (moderately infuscated) . . . . ***avinoviellus***

– Ridge between labral tubercles is, at its mid point, broader than basal depression, with few or many punctures (Figs 221 & 222); wings nearly clear (subhyaline) 4

4 Ridge between labral tubercles subsiding towards middle, where there are often many punctures (Fig. 221); pubescence of thoracic dorsum grey-white or lemon-yellow, but with a broad black band between wings (Figs 242–245, 247, 248, 250, 251) . . . . **himalayanus**

– Ridge between labral tubercles convex for its entire length, with few punctures (Fig. 222); pubescence of thoracic dorsum lemon-yellow, with only a very few black hairs (Figs 254, 255, 257) . . . . **marussinus**

5 (Subgenus *Psithyrus*.) Lateral keels of sternum VI projecting well beyond tergum VI from dorsal aspect, crests of keels sharply acute and blade-like in section, distinctly angled about midway along their length (Figs 207 & 208); pubescence of tergum V usually mostly orange-red, without yellow or white hairs, only occasionally entirely black 6

– Lateral keels of sternum VI not clearly projecting beyond tergum VI from dorsal aspect, crests of keels broadly rounded, both in section and along their entire length (Figs 206, 209–211); pubescence of tergum V black, yellow or white, but without orange-red hairs 7

6 Crests of lateral keels of sternum VI, beyond projecting angle of mid-point, with a strongly concave margin (Fig. 208); sternum II with transverse ridge sharply-defined and nearly straight; labral furrow narrow, about a fifth of total basal breadth of labrum; clypeus with many large punctures spaced more closely than their own widths, except in a well-defined narrowly-unpunctured mid-apical area; pubescence of thoracic dorsum without black hairs, except for a few hairs adjacent to tegulae, tergum II predominantly black (Figs 263, 265, 266) . . . . **branickii**

– Crests of lateral keels of sternum VI, beyond projecting angle of mid-point, almost straight (Fig. 207); sternum II with transverse ridge rounded and curved unevenly towards anterior margin in middle; labral furrow wide, about a third of total basal breadth of labrum (Fig. 24); most of clypeus with scattered large punctures spaced more widely than their own widths; pubescence of thoracic dorsum usually with a poorly-defined patch of black hairs between wings, tergum II yellow (Figs 259 & 261) . . . . **novus**

7 Lateral keels of sternum VI strongly swollen almost to their apices, where they are separated by a groove that is narrower than their own breadths (Figs 209 & 210); basal depression of labrum deep and clearly delimited by an absence of punctures, apex of lamella pointed 8

– Lateral keels of sternum VI declining from near their mid-points so that strongly swollen parts are separated by more than their own breadths (Figs 206 & 211); basal depression of labrum shallow and with punctures, apex of lamella broadly rounded 9

8 Tergum VI with many large punctures, but shining; basal keel of mandible weak or absent; thoracic dorsum without black pubescence (Fig. 267) . . . . **ferganicus**

– Tergum VI with only fine punctures, strongly shining; basal keel of mandible well developed but interrupted before margin of mandible; pubescence of thoracic dorsum black with an admixture of yellow hairs as an anterior band (Fig. 269) . . . . **morawitzianus**

9 Lateral keels of sternum VI small and converging to a point well before apex, which is down-curved as a narrow spinose hook that projects strongly beyond apex of tergum VI (Fig. 211); basal keel of mandible present but interrupted before reaching margin; labral tubercles and lamella weakly developed and rounded in section; oculo-malar distance nearly equal to basal breadth of mandible; pubescence of thoracic dorsum and tergum I predominantly yellow, at most with a narrow band of black hairs between wings (Figs 271 & 273) . . . . **skorikovi**

– [From material from Britain.] Lateral keels of sternum VI strongly swollen and converging to a point only just before apex of sternum, which is broadly triangular and not down-curved or particularly narrowed and does not project beyond apex of tergum VI (Fig. 206); basal keel of mandible weak or absent; labral tubercles pointed and lamella strongly swollen; oculo-malar distance less than two-thirds of basal breadth of mandible; pubescence of thoracic dorsum and tergum I black, with only a broad yellow band anteriorly on thorax . . . . **bohemicus**

10 Apex of mandible broadly rounded, with a basal tooth, one pre-basal tooth and often an apical tooth (e.g. Fig. 34); longest of erect hairs near anterior margin of outer surface of hind basitarsus shorter than greatest breadth of basitarsus 11

– Apex of mandible with six teeth, though these are subject to wear (Fig. 33); longest of erect hairs near anterior margin of outer surface of hind basitarsus just longer than greatest breadth of basitarsus. (Subgenus *Alpigenobombus*, oculo-malar distance about half of basal breadth of mandible; pubescence long, with a broad black band between wings, terga III-V always with some reddish hair, remainder grey-white, yellow or black, Figs 295, 296, 298, 299, 301–303, 305, 306, 308, 309) . . . . **kashmirensis**

11 Hind basitarsus with dense pubescence of proximal margin (auricle) continuing onto outer surface of proximo-posterior projection as just a few sparse hairs (Fig. 229); oculo-malar distance shorter or longer than one and a fifth times basal breadth of mandible, but anterior part of malar area smooth, at most the larger individuals have only a narrow diagonal band with a few very small punctures 12

– Hind basitarsus with dense pubescence of proximal margin (auricle) continuing onto outer surface of proximo-posterior projection as a dense long brush (Figs 227 & 228); oculo-malar distance more than one and a fifth times longer than basal breadth of mandible, and for larger individuals at least, anterior part of malar area uneven with many small to moderately-large but widely-spaced punctures almost throughout 23

12 Disto-posterior corner of mid basitarsus usually broadly rounded, never produced as a spine (Fig. 40); oculo-malar distance shorter or longer than one and a fifth times basal breadth of mandible ..13

– Disto-posterior corner of mid basitarsus spinose (Fig. 39), or for small workers, at least acutely produced; oculo-malar distance at least one and a fifth times longer than basal breadth of mandible 16

13 Ocello-ocular area with unpunctured and shining areas large or small, but area anterior to ocelli unpunctured for less than breadth of an ocellus; labral lamella narrow, only about a third of basal breadth of labrum; clypeus with many large punctures scattered on flattened central area; pubescence of thoracic dorsum with or without much pale hair 14

– Ocello-ocular area with unpunctured and shining areas very large and including most of area anterior to ocelli for a distance of more than breadth of an ocellus (Fig. 215); labral lamella broad, more than half of basal breadth of labrum; clypeus with almost no large punctures in flattened central area; pubescence of thoracic dorsum entirely black. (Subgenus *Orientalibombus*, large individuals with very dark wings; pubescence short and very even, terga I-II bright yellow, III-V orange-red, Figs 279 & 280) .... ***haemorrhoidalis***

14 Band of punctures along eye margin in oculo-ocellar area opposite lateral ocellus with few small punctures, large punctures separated by more than their own widths, whole band occupying about a third of distance between lateral ocellus and eye (Figs 216–219); tergum VI subapically nearly flat, or at most with a poorly-defined apical swelling or a narrow median ridge, but without a discrete subapical rounded boss; wings clear (hyaline), or at most only weakly clouded with brown (weakly infuscated) 18

– Band of punctures along eye margin in oculo-ocellar area opposite lateral ocellus occupying nearly half of distance between lateral ocellus and eye, with many small and large punctures all separated by less than widths of large punctures, or if punctures are mostly large and more widely spaced, then tergum VI has a discrete subapical rounded boss (e.g. Fig. 231, often weak or absent for small workers); wings clear (hyaline) to nearly black (strongly infuscated) 15

15 Oculo-malar distance about equal to or distinctly longer than basal breadth of mandible; tergum VI with a discrete subapical rounded boss (e.g. Fig. 231, often weak or absent for small workers); mandible with only a shallow notch (incisura) and tooth apically (Fig. 34) 24

– Oculo-malar distance less than two-thirds of basal breadth of mandible; tergum VI subapically nearly flat, without a rounded boss; mandible with a deep notch (incisura) and tooth apically 22

16 Clypeus without large punctures in central area; antennal segment 4 longer than broad and more than three-quarters of length of segment 5; pubescence of gaster white, cream, yellow, brown or black, but without orange-red 17

– Clypeus with many large punctures throughout; antennal segment 4 just shorter than broad and less than three-quarters of length of segment 5 (Fig. 17); pubescence of gaster with some orange-red. (Subgenus *Diversobombus*, pubescence of thoracic dorsum black, terga I-II bright yellow, III-V predominantly orange-red, Figs 275, 276, 278) .... ***trifasciatus***

17 (Subgenus *Subterraneobombus*.) Central area of clypeus almost without punctures, at most with only a few very widely-spaced and fine punctures; pubescence of head, lower sides of thorax, legs, all sterna and terga III-V black (Figs 282–284, 286–289) .... ***melanurus***

– Central area of clypeus with many fine punctures, often separated by a distance of only about twice their own diameter; pubescence of thorax almost entirely cream-yellow, except for a black band between wings, and with many pale hairs on head around bases of antennae, on coxae and hind femora, on gastral sterna and as posterior fringes of terga III-V (Figs 291 & 292) .... ***personatus***

18 (Subgenus *Pyrobombus*.) Pubescence of thoracic dorsum grey-white or yellow, but not brown, often with many black hairs, terga IV-V orange-red ...19

– Pubescence of thoracic dorsum uniformly yellow-brown, only occasionally faded to grey, terga IV-V white (Figs 311, 312, 314, 315) ....***hypnorum***

19 Vertex, postero-laterally to ocello-ocular area, shining, with few fine punctures between large punctures (Figs 216 & 217), punctures becoming more numerous and more closely spaced towards posterior margin of vertex (occiput); apex of tergum VI rounded, subacute (Fig. 214) 20

– Vertex, postero-laterally to ocello-ocular area, with many close, fine punctures between large punctures (Figs 218 & 219), punctures uniformly spaced and numerous towards posterior margin of vertex (occiput); apex of tergum VI broadly truncate (Figs 212 & 213) 21

20 Labral lamella narrow, less than one-third of breadth of labrum; hind basitarsus with posterior margin nearly straight in distal half (Fig. 42), stout bristles on outer surface arising from sockets that are scarcely raised from surface; pubescence long, longest hairs of anterior margin of hind tibia much longer than its distal breadth, longest hairs of face at least three-quarters as long as segment 1 (scape) of antenna; pale pubescence of thoracic dorsum either yellow, grey-white or absent, but if it is yellow then

there are no black hairs intermixed (Figs 335, 336, 338, 339, 341, 342, 344–346) .... ***biroi***

– Labral lamella broad, more than one-third of breadth of labrum; hind basitarsus with posterior margin usually distinctly concave just proximal to disto-posterior corner (Fig. 41), stout bristles on outer surface arising from sockets that are strongly raised from surface on their proximal sides; pubescence short, longest hairs of anterior margin of hind tibia only as long as its distal breadth, longest hairs of face only two-thirds as long as segment 1 (scape) of antenna; pale pubescence of thoracic dorsum yellow, with black hairs between wing bases (Figs 317, 319, 320, 322, 323) .... ***subtypicus***

21 Thoracic scutum mid-dorsally with an area as large as tegula around posterior end of longitudinal median groove smooth with few or no punctures (Fig. 224); oculo-malar distance shorter than basal breadth of mandible; hairs of ventral parts of thorax and gaster predominantly grey-white, top and front of head often with many pale hairs intermixed .... ***lepidus***

– Thoracic scutum mid-dorsally with punctures and sculpturing almost throughout area around posterior end of longitudinal median groove (Fig. 223); oculo-malar distance equal to or just longer than basal breadth of mandible (Fig. 15); hairs of ventral parts of thorax and gaster predominantly black, top and front of head without pale hairs .... ***lemniscatus***

22 (Subgenus *Bombus*.) Pubescence of thoracic dorsum grey-white, with a more or less well-developed black band between wings, tergum V red (Figs 347, 348, 350, 351, 353, 354) .... ***tunicatus***

– Pubescence of thoracic dorsum black, with a broad, lemon-yellow or cream anterior band, sometimes with a narrow posterior band, and tergum V nearly white (Figs 356, 357, 359–361, 363, 364, 366, 368, 369) .... ***lucorum***

23 (Subgenus *Sibiricobombus*.) Oculo-malar area with many widely-spaced moderate to large punctures; antennal segment 4 less than half of length of segment 3 (Fig. 19); tergum VI coarsely sculptured but without a median groove .... ***asiaticus***

– Oculo-malar area with many widely-spaced small punctures almost throughout, surface uneven; antennal segment 4 more than half of length of segment 3 (Fig. 20); tergum VI coarsely sculptured, with a well-defined long narrow median groove (Fig. 230) .... ***oberti***

24 (Subgenus *Melanobombus*.) Ocello-ocular areas laterally shining between few large punctures along eye margin opposite ocelli, these punctures separated by distances greater than their own widths; oculo-malar distance longer than, or about same length as, basal breadth of mandible; long hairs of head interspersed with a dense cover of short branched hairs, which are especially evident between ocelli and occiput; pubescence of tergum V usually with some white hairs, or if these are absent, then wings are nearly black (strongly infuscated) 25

– Ocello-ocular areas laterally matt, with a dense band of large punctures along eye margin opposite ocelli, many of these punctures separated by distances less than their own widths; oculo-malar distance just shorter than basal breadth of mandible; only a few short branched hairs interspersed with long hairs on head; wings nearly clear (subhyaline) and pubescence of tergum V usually uniformly red, or if white hairs are present then there are very few black hairs intermixed with pale pubescence on anterior part of thoracic dorsum 27

25 (*rufofasciatus*-group.) Outer (corbicular) surface of hind tibia with only a few short branched hairs, which are confined to margins near disto-posterior corner; pubescence of thoracic dorsum yellow or grey-white, but with a black band between wings; tergum V usually with some white hairs, at least apically; wings nearly clear or lightly clouded with brown (subhyaline to weakly infuscated) 26

– Outer (corbicular) surface of hind tibia with many short to moderately long, branched hairs, at least in proximal half (few or absent for small workers and subject to loss for older females, Fig. 226); pubescence of thorax either entirely black or almost entirely cream-white dorsally and without a black band between wings, tergum V red without any white hairs (Figs 417, 418, 420); wings nearly black (strongly infuscated) .... ***simillimus***

26 Boss on tergum VI nearly circular and evenly convex, only narrowly pointed adjacent to apex of tergum; pubescence of head entirely black, thoracic dorsum and tergum I with white pubescence (Figs 431, 432, 434, 435, 437, 438) .... ***rufofasciatus***

– Boss on tergum VI nearly triangular, for some queens with a weak median groove, for workers it may be weakly ridged; short hairs of head yellow, thoracic dorsum and tergum I with yellow pubescence (Figs 422, 423, 425, 426, 428, 429) .... ***pyrosoma***

27 (*lapidarius*-group.) Ocello-ocular area with a continuous broad band of fine punctures along eye margin; pubescence of thoracic dorsum uniformly lemon-yellow, without black hairs (Figs 397, 398, 400, 401) .... ***semenovianus***

– Ocello-ocular area with band of fine punctures along eye margin narrowly interrupted opposite ocelli, so that there is a small shining area with only large punctures; pubescence of thoracic dorsum pale yellow, cream, or grey-white, but with a broad black band between wings 28

28 Apex of tergum VI usually broadly, but shallowly, notched; pubescence of tergum III predominantly black, often with a posterior fringe of pale hairs, and of tergum V predominantly red (Figs 403–409, 411–415) .... ***keriensis***

– Apex of tergum VI nearly straight; pubescence of tergum III predominantly orange-red and of tergum V white, although these hairs have very dark bases (Figs 394 & 396) .... ***ladakhensis***

Key to species (males)

1 Volsella always strongly sclerotised, inner corner usually much closer to apex than to base (to form an interio-apical corner), often bearing two inwardly-directed hooks or a single combined inwardly-directed process (Figs 136–165); gonostylus usually with a distinct interio-basal process or shelf, but not associated with long hairs (Figs 176–205); head of penis valve much modified, often curved strongly in towards mid-line of body, as a sickle-shaped hook (Figs 61–71, 76–85), otherwise curved outwards for some individuals (Figs 72–75), but if it is nearly straight from dorsal aspect (Figs 56–60), then volsella has pronounced inner hooks (Figs 136–140) 10

– Volsella weakly or strongly sclerotised, inner corner located near mid-point of its length, without any inwardly-directed hooks, so that volsella is usually nearly triangular in the distal section (Figs 126–135); gonostylus without an interio-basal process (Figs 166–169), or if present (Figs 170–175), then it is associated with many long branched hairs; head of penis valve nearly straight from dorsal aspect (Figs 46–55) 2

2 Volsella weakly sclerotised, yellowish in colour; gonostylus with a pronounced interio-basal process (Figs 170–175), associated with many long branched hairs; head of penis valve, as defined by an outer lateral ridge, less than a quarter of total length, not strongly curved but shaped like a slender arrowhead from lateral aspect (Figs 90–95) 5

– Volsella strongly sclerotised, dark brown in colour; gonostylus without an interio-basal process or hairs (Figs 166–169); head of penis valve, as defined by an outer lateral toothed ridge, accounting for nearly half of total length, ventrally curved and sabre-shaped from lateral aspect (Figs 86–89) 3

3 (Subgenus *Mendacibombus*.) Penis valve strongly laterally flattened (Figs 46, 47, 86, 87); gonostylus dorso-ventrally flattened (Figs 166 & 167); mandible with basal tooth strongly developed (Fig. 35); wings clouded with brown (moderately infuscated) . . . . ***avinoviellus***

– Penis valve nearly tubular (Figs 48, 49, 88, 89); gonostylus stout and not strongly flattened (Figs 168 & 169); mandible without a distinct basal tooth; wings nearly clear (weakly infuscated or subhyaline) 4

4 Volsella with interio-apical margin weakly concave (Fig. 128); gonostylus from outer dorso-lateral aspect with a distinct, though broadly-rounded, exterio-apical corner (Fig. 168); pubescence of thoracic dorsum anteriorly and of terga I-II grey-white and/or lemon-yellow, with a broad black band between wings (Figs 246, 249, 252, 253) . . . . ***himalayanus***

– Volsella with interio-apical margin strongly concave, so that apex resembles a curved finger (Fig. 129); gonostylus from outer dorso-lateral aspect with exterio-apical margin evenly rounded, without any trace of an exterio-apical corner (Fig. 169); pubescence of thoracic dorsum lemon-yellow, with few black hairs (Fig. 256) . . . . ***marussinus***

5 (Subgenus *Psithyrus*.) Volsella in its distal section, beyond inner corner, greatly narrowed, almost parallel-sided and finger-shaped (Fig. 135); gonostylus with only a few short hairs . . . . ***skorikovi***

– Volsella distally broader, in the form of a broad nearly triangular plate (Figs 130, 131, 133, 134), or if distal section is narrowed then inner corner is strongly produced (Fig. 132); gonostylus usually with many long hairs around interio-basal process 6

6 Ventro-basal angle of penis valve strongly and broadly produced ventrally and outwardly, so as to be clearly visible from dorsal aspect (Figs 51–54, 91–94); inner corner of volsella well defined, strongly produced for some individuals (Figs 131–134); antennal segment 3 distinctly shorter than segment 5 (e.g. Fig. 22); pubescence of scutellum usually almost entirely yellow or grey, terga IV-V with red or yellow, or if terga IV-V are nearly white (Fig. 270) then tergum II has a narrow apical band of pale hair 7

– Ventro-basal angle of penis valve much reduced and not visible from dorsal aspect (Figs 50 & 90); inner corner of volsella weak, almost unmarked for some individuals (Fig. 130); antennal segment 3 just longer than segment 5 (Fig. 21); pubescence of scutellum black, with only a narrow band of yellow hairs, apical margin of tergum II without a band of pale hair, terga IV-V nearly entirely white (Fig. 258) . . . ***bohemicus***

7 Inner margin of distal section of volsella irregular but not predominantly concave (Figs 133 & 134); antennae very long, reaching back nearly to gaster; pubescence of terga V-VII black, with lateral patches of yellow or white 8

– Inner margin of distal section of volsella predominantly concave, with exception of a weak subapical process (Figs 131 & 132); antennae short, reaching back only to tegulae; pubescence of terga V-VII orange-red 9

8 Distal section of volsella as long as about one and a half times its maximum breadth from ventral aspect (Fig. 133); gonostylus broadly triangular (Fig. 173); pubescence of thoracic dorsum predominantly brownish-yellow, with only a few black hairs above tegulae (Fig. 268) . . . . ***ferganicus***

– Distal section of volsella only just longer than its maximum breadth from ventral aspect (Fig. 134); gonostylus reduced to a narrow transverse band at apex of gonocoxite, but retaining a well-developed interio-basal process (Fig. 174); pubescence of thoracic dorsum light yellow with a broad black band between wings (Fig. 270) . . . . ***morawitzianus***

9 Distal section of volsella almost twice as long as its maximum breadth from ventral aspect (Fig. 132); pubescence of thoracic dorsum yellow, with black hairs intermixed between wings (Fig. 264) . . . . . . ***branickii***

– Distal section of volsella about as long as its maximum breadth from ventral aspect (Fig. 131); pubescence of thoracic dorsum grey-white, with a poorly-defined black band between wings (Figs 260 & 262) . . ***novus***

10 Penis valve from dorsal aspect turned inwards before apex and dorso- ventrally flattened in the form of a sickle (Figs 61–71, 76–85) 11

– Penis valve from dorsal aspect apically nearly straight, turned outwards, or at least not strongly inwardly directed and flattened as a sickle-shape (Figs 56–60, 72–75) 14

11 Ventro-basal angle of penis valve much reduced, shown only as a weak curve, or absent (Figs 116–125); spatha, beyond basal fusion with penis valves, more than three times longer than its breadth midway along this length, sides nearly parallel in proximal half 12

– Ventro-basal angle of penis valve produced as a basally-directed hook (Figs 101–111); spatha, beyond basal fusion with penis valves, less than three times longer than its breadth midway along this length, sides weakly diverging in proximal half (*B. kashmirensis*), or distinctly converging towards apex throughout their length 13

12 Gonostylus just longer than its greatest breadth, excluding interio-basal process, which is pronounced as a broad shelf, and broadening apically (Figs 196–199); shaft of penis valve more than three-quarters as broad from lateral aspect as greatest breadth of gonostylus, excluding its interio-basal process (Figs 116–119); head of penis valve with a broad outer ridge (Figs 76–79, 116–119) 23

– Gonostylus shorter than its greatest breadth, excluding interio- basal process, which is reduced to a small rounded projection or a right-angled corner, and narrowing apically (Figs 200–205); shaft of penis valve usually strongly narrowed from lateral aspect, its breadth less than two-thirds as broad as greatest breadth of gonostylus, excluding interio-basal process (Figs 120–125); head of penis valve with only a narrow outer ridge (Figs 80–85, 120–125) 24

13 Apex of mandible acutely pointed, with a basal tooth and a pre-basal tooth (Fig. 37); gonostylus with a pronounced interio-basal process (Figs 181–183); volsella, from dorsal aspect, projecting beyond gonostylus apically by about its own apical breadth. (Subgenus *Alpigenobombus*, pubescence with a broad black band between wings, head predominantly black, terga III-VI with some reddish hair, remainder variously banded with grey-white, yellow or black, Figs 297, 300, 304, 307, 310) . . . . ***kashmirensis***

– Apex of mandible more or less pointed, otherwise with only a basal tooth; gonostylus without a strongly projecting interio-basal process (Figs 184–191); volsella, from dorsal aspect, projecting beyond gonostylus apically by only about half of its own apical breadth 18

14 Penis valves strongly broadened in dorso-ventral plane so as to form two halves of a tube, ends splayed outwards as a broad funnel (Figs 72–75, 112–115); antennae short, reaching back only as far as tegulae 22

– Penis valves dorso-ventrally narrow, at least in apical third, which is further narrowed and more or less ventrally-directed (Figs 56–60, 96–100); antennae long, reaching back beyond tegulae 15

15 Volsella apically not narrowed, with apical corner forming a right angle, not produced, a projection from inner corner terminating in a single small serrated process, which is directed apically, without any trace of a separate recurved basally-directed hook (Figs 138–140); ventro-basal angle of penis-valve strongly produced ventro-laterally, forming a flattened paddle-shape, transverse to main axis of penis valve (Figs 98–100); pubescence of thoracic dorsum cream, yellow or brown, some individuals with black bands between wings, terga III-VII without orange-red 17

– Volsella apically much narrowed, or with apical corner narrowly produced, inner corner terminating in a pair of serrated hooks, one directed apically, the other, which may be very much reduced for some individuals, directed basally (Figs 136 & 137); ventro-basal angle of penis valve produced ventrally, but hardly laterally, as a single tooth (Figs 96 & 97); pubescence of thoracic dorsum black, terga III-VII predominantly orange-red 16

16 Gonostylus with interio-basal process strongly produced, with both an apically-directed hook and a more ventrally-directed hook (Fig. 176); volsella with inner hooks very close to apical corner, the large apically-directed hook nearly straight and spinose, the basally-directed hook strongly recurved and broad with many teeth, both hooks projecting beyond gonostylus from dorsal aspect, part of volsella immediately proximal to inner hooks much narrowed (Fig. 136); head of penis valve twice as broad as shaft, from dorsal aspect, with pronounced teeth along outer lateral ridge (Fig. 56) (Subgenus *Diversobombus*) . . . . ***trifasciatus***

– Gonostylus without an interio-basal process (Fig. 177); volsella with apical corner narrowly produced distal to inner hooks and curled inwardly, inner hooks close to inner corner and obscured from dorsal aspect by gonostylus, part of volsella immediately proximal to inner hooks broad (Fig. 137); head of penis valve scarcely broader than shaft, from dorsal aspect, without distinct teeth along lateral ridge (Fig. 57) (Subgenus *Orientalibombus*) . . . . ***haemorrhoidalis***

17 (Subgenus *Subterraneobombus*.) Curved head of penis valve, from dorsal aspect, longer than broad (Figs 58 & 59), paddle-like ventro-basal angle of penis valve clearly tridentate, with a spinosely-produced dorso-lateral tooth, which is longer than tooth that some individuals have on exterio-basal corner of penis valve head (Figs 98 & 99); tip of

interio-basal process of gonostylus not projecting apically as far as apex of gonostylus (Figs 178 & 179); pubescence of head around antennal bases, of ventral parts of thorax and of terga III-VII, predominantly black (Figs 285 & 290) . . ***melanurus***

– Curved head of penis valve, from dorsal aspect, as broad as long (Fig. 60), paddle-like ventro-basal angle of penis valve almost rounded, with only a weak dorso-lateral tooth, which is shorter than spinose tooth of exterio-basal corner of penis valve head (Fig. 100); tip of interio-basal process of gonostylus projecting apically as far as apex of gonostylus (Fig. 180); pubescence of head around antennal bases, of ventral parts of thorax and of posterior fringes of terga III-VII predominantly pale (Figs 293 & 294) . . . . ***personatus***

18 (Subgenus *Pyrobombus*.) Inner margin of gonostylus weakly convex basally, longitudinal submarginal groove arising close to apex of gonocoxite, separated from it by a distance usually only about equal to width of groove (Figs 185–191); pubescence of terga V-VII orange-red 19

– Inner margin of gonostylus with a deep concavity or notch basally, separating longitudinal submarginal groove from apex of gonocoxite by a distance nearly twice width of groove (Fig. 184); pubescence of terga V-VII white (Figs 313 & 316) . . . . . ***hypnorum***

19 Antennae short, reaching back only as far as tegulae; head of penis valve with recurved hook not distinctly narrower than adjacent penis valve shaft, from dorsal aspect, and apically broadly rounded (Figs 67–71); pubescence long, longest hairs arising from outer surface of proximal part of mid basitarsus nearly one and a half times breadth of mid basitarsus 20

– Antennae moderately long, reaching back to scutellum; head of penis valve with recurved hook distinctly narrower than adjacent penis valve shaft, from dorsal aspect, and apically acute (Figs 65 & 66); pubescence short, longest hairs arising from outer surface of proximal part of mid basitarsus shorter than breadth of mid basitarsus . ***subtypicus***

20 Penis valve head with recurved hook no greater in breadth than adjacent penis valve shaft, from dorsal aspect (Figs 67–69), and ventro-basal angle of penis valve close to mid-point between penis valve head and its base (Figs 107–109); pale pubescence with grey-white hair, or if this is lacking (i.e. pubescence predominantly yellow), then tergum III is yellow or orange-red with very few black hairs 21

– Penis valve head with recurved hook more than one and a half times breadth of adjacent penis valve shaft, from dorsal aspect (Figs 70 & 71), and ventro-basal angle of penis valve at less than a third of length of penis valve shaft from its base to its head (Figs 110 & 111); pale pubescence without grey-white hair, tergum III predominantly black (Figs 337, 340, 343) . . . . ***biroi***

21 Pubescence of thorax and tergum I predominantly yellow, without grey-white hairs (Figs 329 & 332); volsella with interio-apical process narrow and separated from apex by a distance nearly equal to its own breadth (Figs 148 & 149) . . . . ***lepidus***

– [From material from Uttar Pradesh, India.] Pubescence of thoracic dorsum and tergum I grey-white, without yellow hairs, but with a broad black band between wing bases; volsella with interio-apical process arising directly from apex (Fig. 147) . . . . ***lemniscatus***

22 (Subgenus *Bombus*.) Pubescence of thoracic dorsum grey-white, often with a more or less well-developed black band between wings, terga V-VI red (Figs 349, 352, 355) . . . . ***tunicatus***

– Pubescence of thoracic dorsum with lemon-yellow anteriorly, remainder with variable degrees of replacement of black by yellow, terga V-VI nearly white (Figs 358, 362, 365, 367, 370) . . . . . . ***lucorum***

23 (Subgenus *Sibiricobombus*.) Eyes greatly enlarged, so that separation from lateral ocelli is by less than an ocellar diameter; antennae very long, reaching almost to gaster; volsella narrowed apically, interio-apical process narrow and elongate but exterio-apical corner scarcely acute (Figs 156–158); recurved hook of penis valve head broad, tapering to tip (Figs 76–78); pubescence short . . . . ***asiaticus***

– [From material from the Pamir, U.S.S.R.] Eyes similar in relative size to those of females, not enlarged, and separated from lateral ocelli by more than two ocellar diameters; antennae long, but reaching only just past tegulae; volsella broadened subapically, interio-apical process very short and broad but exterio-apical corner strongly produced as a broad tooth (Fig. 159); recurved hook of penis valve head narrowly constricted (Fig. 79); pubescence long . . . . ***oberti***

24 (Subgenus *Melanobombus*.) Gonostylus with apical margin concave, leaving an exterio-apical corner and an interio-apical process, latter often with two apical corners or bidentate (Figs 203–205); volsella extending beyond gonostylus apically by at least nearly twice its own breadth at the point where it emerges from beneath gonostylus from dorsal aspect 25

– Gonostylus with apical margin broadly convex (Figs 200–202); volsella extending beyond gonostylus by about its own breadth at the point where it emerges from beneath gonostylus from dorsal aspect 27

25 (*rufofasciatus*-group.) Gonostylus about a third as long in middle as broad, excluding interio-basal process, and reduced to a transverse band, with interio-apical corner extended as a spinose or bilobed process (Figs 204 & 205); pubescence of tergum II extensively lemon-yellow 26

– Gonostylus more than half as long in middle as broad, excluding exterio-basal process, nearly rectangular, with interio-apical corner not strongly produced (Fig. 203); pubescence of tergum II either nearly white or chocolate brown, but not yellow (Figs 419 & 421) .... ***simillimus***

26 Eyes distinctly enlarged relative to those of females, separated from lateral ocelli by one ocellar diameter; interio-basal process of gonostylus with apex forming nearly a right angle, interio-apical process with sides diverging towards apex, which is broadly bilobed (Fig. 205); pale pubescence of thorax and tergum I grey-white (Figs 433, 436, 439) .... ***rufofasciatus***

– Eyes not enlarged relative to those of females, separated from lateral ocelli by two ocellar diameters; interio-basal process of gonostylus with apex distinctly acute, interio-apical process with sides often converging towards apex (Fig. 204), which may be spinose even from outer lateral aspect; pale pubescence of thorax and tergum I yellow (Figs 424, 427, 430) .... ***pyrosoma***

27 (*lapidarius*-group.) Eyes slightly enlarged relative to those of females, separated from lateral ocelli by less than two ocellar diameters; pubescence of thoracic dorsum uniformly lemon-yellow, without black hair (Figs 399 & 402) .... ***semenovianus***

– Eyes not enlarged relative to those of females, separated from lateral ocelli by about two and a half ocellar diameters; pubescence of thoracic dorsum pale yellow with a black band between wings 28

28 Free, recurved hook of penis valve head about two-thirds as long as more apical part of penis valve head (Fig. 82), penis valve shaft narrower at its mid-point from lateral aspect (Fig. 122) than spatha is at its mid-point from dorsal aspect; pubescence of tergum III black, at most with only a narrow apical and lateral fringe of pale hairs, terga IV-VII orange-red (Figs 410 & 416) .... ***keriensis***

– Free, recurved hook of penis valve head about one-third as long as more apical part of penis valve head (Fig. 80), penis valve shaft broader at its mid-point from lateral aspect (Fig. 120) than spatha is at its mid-point from dorsal aspect; pubescence of terga III-V predominantly orange-red, terga VI-VII predominantly pale, hairs nearly white with orange bases, black hairs mostly confined to basal margin of tergum III, otherwise intermixed on lateral quarters of remaining terga (Fig. 395) .... ***ladakhensis***

Genus ***BOMBUS*** Latreille

[*Bremus* [Jurine], 1801: 164. Type species: *Apis terrestris* Linnaeus, 1758: 578 = *Bombus terrestris* (Linnaeus), by subsequent designation of Morice & Durrant (1915: 429). Suppressed by the ICZN in Opinion 135 (ICZN, 1939).]

[*Bremus* Panzer, [1801]: pls. 19–21. Type species: *Apis agrorum* Fabricius, 1787: 301 = *Bombus pascuorum* (Scopoli), by subsequent designation of Sandhouse (1943: 532). Suppressed by the ICZN in Opinion 220 (ICZN, 1954).]

Bombus Latreille, 1802*a*: 437 [redescribed 1802*b*: 385]. Type species: *Apis terrestris* Linnaeus, 1758: 578 [cited as *Apis terrestris* F.] = *Bombus terrestris* (Linnaeus), by monotypy.

Specialists often find it useful to be able to refer to groups of closely related species by group-names. The use of the established subgeneric names as labels for assemblages of similar bumble bee species is continued here solely for the sake of nomenclatural continuity, because there is little advantage at present in modifying the usage of previous authors (see the introduction on genera of Bombini). When it is possible to revise all of the bumble bees thoroughly, this system could be replaced or at least simplified. For this review, only a few additions and revisions to a preliminary cladistic study of relationships (Williams, 1985) are included in the discussions of affinities for each species. As little as possible is added to the burden of subgeneric nomenclature, although the application of certain names does require some clarification.

Richards (1968) described the characteristics of both sexes for species of the subgenera referred to here, with the exception of *Psithyrus*, which is described by Popov (1931) and by Løken (1984).

Subgenus ***MENDACIBOMBUS*** Skorikov

Mendacibombus Skorikov, 1914*a*: 125. Type species: *Bombus mendax* Gerstaecker, 1869: 323, by subsequent designation of Sandhouse (1943: 572).

Mendacibombus Skorikov; Krüger, 1917: 62 (as a subgenus of *Bombus* Latrielle).

Species of the subgenus *Mendacibombus* have been regarded as showing the most plesiomorphic forms of the male genitalia among bumble bees (Williams, 1985). A brief review of most species of this group is now possible thanks to generous loans of material from other institutions (ITZ, MNHU, ZI). These nominal taxa have been described from female type specimens, which are all closely similar in morphology (e.g. mostly described as subspecies of *B. mendax* by Skorikov, 1910*a*). The application of the names to the more divergent males naturally depends on correct association of the sexes. For these associations I have relied on reference material from A. S. Skorikov's collection (ZI, with a few specimens in the BMNH), because he had access to relatively large samples of material and had described many of the taxa himself.

The results of a cladistic analysis show that the subgenus *Mendacibombus* is likely to be paraphyletic with respect to all other bumble bees (Fig. 5, all other bumble bees represented by *B. exil*, see the comments on *B. avinoviellus*, *B. himalayanus* and *B. bohemicus*). This is a change in the interpretation of relationships within this species-group (see the introduction on generic nomenclature) that results from a change in the interpretation of the broadened state of the inner lateral shelf of the penis valve. This character is at best weakly developed in species of the out-group, Euglossini, which have the shaft of the penis valve much shorter. If the strong development of the shelf is regarded as plesiomorphic rather than apomorphic within the subgenus *Mendacibombus*, then its compatibility with the additional character state patterns in this analysis is maintained. Holophyletic groups within the paraphyletic subgenus *Mendacibombus* are largely single species (monotypic) or unresolved. For a general description of both sexes of the species of this subgenus see Richards (1968) and the keys (couplets 1 & 2).

The North American *B. (Bombias) nevadensis* Cresson is similar to species of the subgenus *Mendacibombus* in the simple, straight form of the penis valves (see Milliron, 1971: pl. 11) and in the enlarged compound eyes of the male. However, at present the weight of evidence does not support a particularly close relationship by descent. On the one hand, the shared form of the penis valves is interpreted as a symplesiomorphy among the bumble bees and the enlarged eyes of the males are likely to be a convergent character state. Alcock & Alcock (1983) related the enlarged eyes of male *B. nevadensis* to the particular kind of mate-searching behaviour that they employ. Among the Kashmir fauna, this behaviour is apparently related in turn more to habitat structure than to relationships by ancestry (see the introduction on the relationship of male eye-size to mate-searching behaviour and habitat structure, also see the comments on the species of the *rufofasciatus*-group: *B. simillimus*, *B. pyrosoma* and *B. rufofasciatus*). Thus neither the shape of the penis valve nor the shape of the eyes can be used as evidence of close relationship. On the other hand, *B. nevadensis* has a flattened form of the male gonostylus that has a distinct interio-basal process. More particularly this species has a strongly narrowed form of the volsella that has a narrowly subapical and broad, many-toothed, interio-apical process. *B. nevadensis* appears to share these character states (?synapomorphies) with species such as *B. (Alpinobombus) arcticus* (Quenzel) (oldest available name for *B. hyperboreus* Schönherr), rather than with any species of the subgenus *Mendacibombus*. Consequently this species is not included here in the subgenus *Mendacibombus*.

The males of the European and central Asian *B. (Confusibombus) confusus* Schenck also have relatively simple, straight heads of the penis valves and enlarged compound eyes. Because of this similarity, *B. confusus*, like *B. nevadensis*, has sometimes been grouped with *B. mendax* (e.g. Kruseman, 1952). However, both *B. confusus* and *B. nevadensis* share the development of an inwardly-directed process from the base of the gonostylus with most bumble bees apart from species of the subgenus *Mendacibombus* (synapomorphy of *Psithyrus* + all other subgenera of *Bombus* excluding *Mendacibombus*). Ito (1985) concluded from his detailed phenetic study that *B. nevadensis* is most closely similar to *B. confusus*, and then to *B. (Kallobombus) soroeensis*, followed by species of the subgenera *Rhodobombus* or *Alpinobombus*. Evidence from biochemical characters would be particularly useful in these cases.

Within the subgenus *Mendacibombus*, nests have been described in detail for only the European *B. mendax* (by e.g. Haas, 1976; see also a brief footnote on a nest of *B. makarjini* by Reinig *in* Bischoff, 1931). These nests appear to show a greater resemblance in their structure to nests of some stingless bees (cf. Wille & Michener, 1973) than do those of other bumble bees. In particular, the cocoons are almost completely torn down soon after the emergence of the adults, so that pollen and honey must be stored elsewhere. In contrast to other bumble bees, these food reserves are held exclusively outside the wax envelope of the brood nest and the honey may be stored in hexagonally arranged wax cells.

Bombus (Mendacibombus) avinoviellus (Skorikov)

(Figs 14, 16, 23, 27, 31, 35, 43–47, 86, 87, 126, 127, 166, 167, 220, 225, 232–241, Maps 5 & 6)

Mendacibombus avinoviellus Skorikov, 1914*a*: 126. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, INDIA: Kashmir, Baltal, 11.vi.1912 (*Jacobson*) (ZI) [examined].

Bombus niveatus subsp. *callophenax* Cockerell, 1917: 122. Holotype queen by monotypy (see Note 2 below), INDIA: Kashmir, no further data (*Woglum*) (USNM) [examined]. **Syn. n.**

Bombus (Mendacibombus) avinoviellus (Skorikov); Richards, 1930: 635.

[*Bombus (Mendacibombus) avinoviellus* var. *subtunicatus* Richards, 1930: 635 [examined]. Infrasubspecific (see Note 1 below) (Art. 45g (ii)(1)), unavailable name (Art. 45e).]

NOMENCLATURE. Note 1. Richards's use (1930:

634 etc.) of the term 'Subsp.' elsewhere in his paper is taken to indicate that infrasubspecific rank is meant for *B. avinoviellus* var. *subtunicatus*.

TYPE MATERIAL. Note 2. Cockerell's description of *B. niveatus callophenax* gives no reason to believe that he had based his description on more than one specimen. Only a single queen in the USNM collection agrees with the original description and carries the data quoted (Dr B.B. Norden, *in litt.*) and this specimen bears a red label 'Type'. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. *B. avinoviellus* is easily distinguished from the other species of the subgenus *Mendacibombus* (and from all other bumble bees) by the laterally compressed and scythe-like heads of the penis valves, which have the weakly-sclerotised lateral channel relatively narrow (Figs 46, 47, 86, 87) (plesiomorphic within the bumble bees, Bombini, and shared with the South American orchid bees, Euglossini).

The closest relatives of *B. avinoviellus* are probably *B. mendax* Gerstaecker and *B. makarjini* Skorikov (Fig. 5). *B. mendax* has the head of the penis valve not laterally compressed as for *B. avinoviellus*, but rounded and finger-like, with a narrowly subapical shoulder on the inner margin from the dorsal aspect. The gonostylus is expanded ventrally along its interio-apical margin, so that it is particularly stout (synapomorphies of *B. mendax* with all species of *Mendacibombus* excluding *B. avinoviellus*; the gonostylus may be secondarily slightly narrowed for *B. makarjini* and the species of the *defector*-group, *handlirschianus*-group and *waltoni*-group, see the comments on *B. himalayanus*). *B. mendax* is known from the European Alps and the Pyrenees (BMNH, PW). *B. makarjini* has the head of the penis valve even more strongly dorso- ventrally compressed than for *B. mendax* and the penis valve head is relatively shorter. The head of the penis valve is defined by an outer toothed ridge (e.g. Fig. 86), which for *B. makarjini* extends for only half of the distance from the apex to the ventro-basal angle of the penis valve. The apex of the volsella is strongly concave on the inner margin so that the apex is narrowed and inwardly curved (synapomorphies of *B. makarjini* with all species of *Mendacibombus* excluding *B. avinoviellus* and *B. mendax*). *B. makarjini* is known from the region of the Pamir and the Tien Shan ranges, where it is uncommon (Reinig, 1930; Skorikov, 1931; Panfilov, 1957; ITZ, ZI). All the other species of the subgenus *Mendacibombus* have the penis valve narrowed basally, particularly by the reduction of the inner lateral shelf (Figs 48 & 49) (synapomorphy; see the comments on *B. himalayanus*).

B. niveatus subsp. *callophenax* was described by Cockerell from a queen that is closely similar in morphology and in its banded white colour pattern to the paralectotype of *B. avinoviellus*. There is no reason to believe that Cockerell was aware of Skorikov's description of *B. avinoviellus*. These two nominal taxa have not previously been recognised as conspecific because most authors have followed the opinion of Richards (1930: 652) that *B. niveatus* subsp. *callophenax* belonged to a taxon of the subgenus *Sibiricobombus* that has a similar, banded white colour pattern. This is a misidentification (see the comments on *B. asiaticus*).

A queen from the Karakoram range (Fig. 232), kindly lent to me by B. Tkalců, resembles *B. marussinus* in the unbanded yellow colour pattern of the pubescence (Fig. 254). However, this queen is otherwise closely similar in its morphological characteristics (see the key), as well as in the stronger clouding of the wings with brown, to the paralectotype queen of *B. avinoviellus* (see the comments on *B. marussinus*). It is therefore considered likely to be part of the same species as *B. avinoviellus*. More material, especially of the males, is needed in order to establish its status definitively.

DISTRIBUTION. *B. avinoviellus* is a west Himalayan species (Map 5). It is known only from Uttar Pradesh (BMNH), Himachal Pradesh (BMNH, PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. avinoviellus* has been recorded from the southern side of the Great Himalaya range, and from the Pir Panjal and Karakoram ranges, primarily in mesic subalpine scrub and in meadows in the upper montane coniferous forest zone (Map 6, Fig. 6): 29 queens, 69 workers, 80 males, from 12 localities 1900–4600 m (BMNH, BT, IZ, LK, MNHN, NR, PW, SEMK, USNM, ZI, ZM).

VARIATION WITHIN KASHMIR. The only specimen of *B. avinoviellus* examined from the Karakoram range, a queen from Banidas (Fig. 232), has the thoracic dorsum, tergum I and the basal margin of tergum II uniformly lemon-yellow, with only a few black hairs above the wing bases.

Individuals from around the Kishanganga valley have the thoracic dorsum dull yellow, with the exception of a band of black hairs between the wing bases (Figs 233–235). Individuals from around the Vale of Kashmir have the pale pubescence of the thoracic pubescence grey-white rather than yellow

(Map 6, Figs 236–241), although there is often some yellow on terga I-II (Figs 236 & 237). Both banded yellow individuals and banded white individuals were taken together at Chittakatha Sar (banded yellow: 2/4 males; banded white: 2/4 males) and at Lal Pani (banded yellow: 5/6 workers, 28/35 males; banded white: 1/6 workers, 7/35 males) in the upper Kishanganga valley, and at Nigagar (1 banded yellow worker, 1 banded white male, 2 banded cream males) in the upper Sind valley.

The individuals with an unbanded yellow thoracic dorsum (Fig. 232) are particularly closely similar in colour pattern to those of *B. marussinus* (Figs 254 & 255), which may occur with them. They are also similar to some individuals of *B. branickii* (Fig. 265), *B. subtypicus* (Fig. 319–324), *B. biroi* (Figs 335–337), *B. asiaticus* (Figs 371–376) and *B. semenovianus* (Figs 397–402). The banded yellow individuals from the Kishanganga valley (Figs 233–235) resemble the local, banded yellow *B. subtypicus* (Figs 317 & 318), *B. asiaticus* (Figs 377, 378, 382) and *B. keriensis* (Fig. 414–416). The banded white individuals from around the Vale of Kashmir (Figs 239–241) are closely similar in colour pattern to the *B. asiaticus* that occur with them (Figs 386, 387, 389–391), but also show some similarity to some banded white individuals of *B. kashmirensis* (Figs 306–310), *B. biroi* (Fig. 342), *B. tunicatus* (Figs 350, 353, 355) and *B. keriensis* (Figs 408 & 409, see also the comments on *B. subtypicus*). *B. avinoviellus* can be recognised by the presence of pale pubescence on the face, by the clouded wings, by the subgeneric and specific characters (see the key, couplets 1–3) and by its small size.

FOOD PLANTS. (Ranunculaceae) *Aconitum heterophyllum* Wallich ex Royle; (Balsaminaceae) *Impatiens glandulifera* Royle; (Hippocastanaceae) *Aesculus indica* (Colebr. ex Cambress.) Hook.; (Leguminosae) *Trifolium repens* L.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., unidentified dandelion-like composites; (Oleaceae) *Syringa emodi* Wallich ex Royle; (Scropulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced]; (Labiateae) *Phlomis bracteosa* Royle ex Benth., *Stachys sericea* Wallich ex Benth., *Prunella vulgaris* L.

Bombus (Mendacibombus) himalayanus (Skorikov)

(Figs 48, 88, 128, 168, 221, 242–253, Maps 7 & 8)

Mendacibombus varius Skorikov, 1914*a*: 125. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, INDIA: Kashmir, Zoji La, above 3000 m, 12–15.vi.1912 (*Jacobson*) (ZI) [examined]. Junior secondary homonym in *Bombus* of *Psithyrus varius* Lepeletier, 1832 [= *B. campestris* (Panzer)].

Mendacibombus mendax subsp. *himalayanus* Skorikov, 1914*a*: 127. Holotype queen by monotypy (see Note below), INDIA: Kashmir, Ladakh, Khardung La, 4500 m, 3.vii.1912 (*Jacobson*) (ZI) [examined]. Provisional synonym.

Bombus (Mendacibombus) mendax subsp. *himalayanus* (Skorikov); Richards, 1930: 635.

TYPE MATERIAL. Note. Skorikov specifies that he made his original description of *Mendacibombus mendax* subsp. *himalayanus* from a single female specimen. Only a single queen in the ZI collection agrees with the original description and carries the data quoted. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. In addition to *B. avinoviellus*, *B. mendax* and *B. makarjini* (see the comments on *B. avinoviellus*), there are at least eight species of the subgenus *Mendacibombus* that are known from both sexes. These species share forms of the penis valve that are narrowed at the base, particularly by the reduction of the inner lateral shelf (Figs 48 & 49) (synapomorphy). This character state is also shared with all the other bumble bees.

Three putative species, *B. himalayanus*, *B. marussinus* and *B. turkestanicus* Skorikov, are found in the mountain system of the western Himalaya, the Hindu Kush, the Pamir and the Tien Shan ranges (see below). Their relationships are not fully resolved (Fig. 5). No synapomorphies are known from which these bees can be recognised as a true, monophyletic group, yet they are morphologically closely similar and they lack the synapomorphies of the remaining species of the subgenus *Mendacibombus*. Among these other species may be recognised the *defector*-group, a possible *handlirschianus*-group and the *waltoni*-group. The latter three groups share with all other bumble bees (see the comments on *B. bohemicus*) a further narrowing and straightening of the penis valve base, with some development of a small semi-circular projection from the inner basal part of the penis valve by a more pronounced reduction of the inner lateral shelf, together with a reduction of the outer lateral shelf (synapomorphies, least well developed for males of the *handlirschianus*-group, also only weakly evident for some species of other subgenera of *Bombus*).

The *defector*-group includes at least *B. defector* Skorikov, for which the penis valve is elongated beyond the volsella and the volsella is particularly broad basally, so that its inner angle is only very broadly rounded (?autapomorphies). *B. defector* may be conspecific with similar females described by Skorikov under the name *B. mendax* subsp. *margreiteri* Vogt, which have the corbicular fringes orange rather than black, and possibly also with females described by Skorikov under the name *B. mendax* subsp. *altaicus*, which have the pale pubescence lighter in shade as well as the corbicular fringes orange. I have not seen any males that can definitely be associated with either of these two nominal taxa. Bees of the *defector*-group are known from the northern Pamir and Tien Shan ranges (Skorikov, 1931; Panfilov, 1957; BMNH, PW, ZI). They may also occur in some of the mountains that extend north-eastwards as far as the other localities known for these bees in Kamchatka (Bischoff, 1930; Skorikov, 1931).

The *handlirschianus*-group may include two species, for which the basal angle of the penis valve is more pronounced and fully ventral rather than lateral, and the gonostylus is narrowed apically (synapomorphies of the *handlirschianus*-group + *waltoni*-group + all other subgenera of *Bombus*, for which they may be secondarily much modified). This is not a true group in that no exclusive synapomorphies are known for the included species, yet they lack the apomorphic character states of the *waltoni*-group and of the other subgenera of *Bombus*. Females of *B. handlirschianus* Vogt have the pale pubescence grey-white. Other females, described by Skorikov under the name *B. mendax* subsp. *shaposhnikovi*, are known from the same area of distribution but have the pale pubescence yellow. It is possible that the white females are part of the same species as those with yellow bands (cf. comments on colour variation of *B. keriensis*). However, the only male of this species- group that I have seen with the pale pubescence white rather than yellow (ITZ) also has the whole gonostylus and the apex of the volsella distinctly broader than it is for the yellow males (see also Skorikov, 1931: figs 14 & 15). Therefore the yellow and the white bees are likely to belong to two separate species, *B. shaposhnikovi* and *B. handlirschianus* respectively. Both of these species of the *handlirschianus*-group are known from Turkey, the Caucasus and the Elburz mountains of Iran (e.g. Reinig, 1971; BMNH, ITZ).

Species of the *waltoni*-group share with most other groups of bumble bees the development of a dorsal toothed ridge on the volsella (see Skorikov, 1931: fig. 20), which, from the ventral aspect, projects beyond the inner margin (synapomorphy of the *waltoni*-group + all other subgenera of *Bombus*, possibly secondarily reduced for *B. (Eversmannibombus) persicus* Radoszkowski and for species of *Psithyrus*). The species of the *waltoni*-group share a very strongly curled apex of the volsella (synapomorphy). The male gonostylus of *B. waltoni* Cockerell is uniquely much broader at the apex than at the base and is dorsoventrally more flattened (autapomorphy). *B. waltoni* is conspecific with *B. mendax* subsp. *chinensis* Skorikov (junior secondary homonym in *Bombus* of *Apathus rupestris* var. *chinensis* Morawitz), and is probably also conspecific with *B. rufitarsus* Friese (see Skorikov, 1914*a*), and with *B. asellus* Friese. *B. waltoni* is known from Tibet (Cockerell, 1910; Friese, 1918; Richards, 1930; Wang, 1982; BMNH), Qinghai (Morawitz, 1886; Skorikov, 1910*a*, 1912*b*; Bischoff, 1936; Wang, 1982; ZI) and Sichuan (Wang, 1982). A record for Mongolia (Friese, 1924) needs confirmation. *B. convexus* Wang (oldest available name for *B. lugubris* Morawitz, 1880, **syn. n.**, which is a junior secondary homonym in *Bombus* of *Psithyrus lugubris* Kriechbaumer, 1870 [= *B. maxillosus* Klug]) has the gonostylus narrow and finger-like (?plesiomorphic within this group), but the apex of the volsella is strongly elongated (autapomorphy). *B. convexus* is known from Tibet (Wang, 1979, 1982; PW), Qinghai (Wang, 1982), Sichuan (Morawitz, 1890), Gansu (Morawitz, 1880, 1890; Bischoff, 1936; MNHU, ZI) and Beijing (Panfilov, 1957). Another species that may belong to this group was described from a single female from the mountains of northern Mongolia (*Mendacibombus superbus* Tkalců, 1968*a*). This individual is unusually large for a species of the subgenus *Mendacibombus*.

B. himalayanus, *B. marussinus* and *B. turkestanicus* appear to differ from one another only in colour pattern (Skorikov, 1910*a*, 1914*a*), in subtle differences in the male genitalia (Figs 48, 49, 168, 169, 128, 129) and in details of female sculpturing (Figs 220–222). Nonetheless these differences are apparently maintained in combination at sites where they are recorded together. For instance, two queens and three workers from Chhantir Gah in the Hindu Raj range are assigned in this review to *B. marussinus*. If these workers were considered together with the material from the same locality that is ascribed to *B. himalayanus*, all of the workers could be interpreted as representing almost a continuum in colour variation between the extreme individuals with an unbanded yellow thorax (originally described under the name *B. mendax* subsp. *marussinus*) and those with a banded white thorax (described under the name *Mendacibombus varius*). However, the workers with a black band on the thoracic dorsum (both *Mendacibombus varius* and *Mendacibombus* *mendax* subsp. *himalayanus*) do have more punctures on the labral ridge, which, although broad, is also particularly weakly raised near its mid-point (Figs 220–222). This combination of character states is strictly maintained where the two taxa occur together at Holojut as well as at Chhantir Gah. Therefore there is no evidence of hybrids from interbreeding between *B. himalayanus* and *B. marussinus*, so they are considered to be separate species (see the comments on *B. marussinus*). There is a similar lack of obvious hybrids as evidence for interbreeding between *B. himalayanus* and *B. turkestanicus*, although I have not seen any samples from single localities that include both taxa. From the material available, *B. himalayanus* always retains the particularly weak labral ridge with many punctures in combination with a tendency towards black pubescence on the lower sides of the thorax and on the legs, both of which distinguish it from *B. turkestanicus*.

A single male with a yellow thorax with black hairs between the wing bases from Kilian (Raskam range, Xinjiang, China) was ascribed by Skorikov (1914*a* : 127) to *Mendacibombus mendax* subsp. *himalayanus* s.str. Unfortunately this specimen could not be found in the ZI collection (M. Podbolotskaya, *in litt.*). This could be the same individual from the 'Raskemkette, Nordhang des Kilieng' that Skorikov later listed under the name *Mendacibombus makarjini* (see Skorikov, 1931: 215). I have seen only two queens of *B. himalayanus* s.str. from Ladakh. These do differ from queens of *B. makarjini*, but resemble queens of *Mendacibombus varius* (Fig. 222), in the more coarsely punctured middle section of the labral ridge.

A comparison of much more material of *B. himalayanus* s.str. with *Mendacibombus varius*, *B. turkestanicus* and *B. makarjini*, especially for the males, is still needed. From the meagre evidence available at present, I consider that *B. himalayanus* s.str. is most likely to be part of the same interbreeding population and species as *Mendacibombus varius*, which is likely to be separate from *B. turkestanicus* and *B. makarjini*.

DISTRIBUTION. *B. himalayanus* is a west Himalayan species (Map 7). It is known from Himachal Pradesh (BMNH, PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. *B. himalayanus* is widespread in Kashmir, where it is recorded from the Hindu Raj, Ladakh, Zanskar, Great Himalaya, and Pir Panjal ranges, in alpine scrub and steppe (Map 8, Fig. 6): 15 queens, 70 workers, 12 males, from 13 localities 2700–4800 m (BMNH, NR, PW, SEMK, ZI, ZM; 1 male photographed in the Sangisfaid valley, C. A. Chadwell).

VARIATION WITHIN KASHMIR. Two queens from the Ladakh and Zanskar ranges (Map 8) have the pale pubescence yellow, with a band of black hairs between the wing bases and black basally on tergum III. The queen from Nimaling has a pronounced black band between the wing bases (Fig. 242), but Skorikov's queen from the Khardung La has only a poorly-defined black band on the thorax (cf. *B. marussinus*). Five workers from Chhantir Gah in the Hindu Raj range have the thoracic band well defined, but the black band on the gaster is much reduced (Fig. 243). In common with many workers in this species-group (but not among queens, except for *B. turkestanicus*), these workers have many pale hairs ventrally.

Also from Chhantir Gah, another queen and eight workers have a similar pattern, although the yellow of the thorax, and to a variable extent on tergum II, is replaced by grey-white. These specimens, and other similar individuals from elsewhere in the Hindu Raj range (Figs 244, 245, 247, 248), have tergum III almost entirely orange-red. This banded white and yellow pattern is predominant among individuals in the samples from the mountains around the Kishanganga valley and the Vale of Kashmir (Figs 246 & 249). However, many of these individuals show some replacement of the pale band at the rear of the thorax by black hairs and black is also more extensive on tergum III, so that it may form a distinct black band on the gaster (Figs 250–252). The single male from Sangisfaid valley is even more extreme, in that all of the orange-red pubescence of the gaster appears to have been replaced by black (Fig. 253).

The yellow individuals of this species (Figs 242 & 243) are similar in colour pattern to the *B. kashmirensis* (Figs 295–300), *B. lepidus* (Figs 327 & 328), *B. oberti* (Figs 392 & 393), *B. ladakhensis* (Figs 394 & 396) and *B. keriensis* (Figs 412 & 413) that occur with them. The white and yellow individuals (Figs 244–252) are similar to the *B. novus* males (Figs 260 & 262), *B. kashmirensis* (Figs 301–304), *B. lemniscatus* (Figs 325 & 326), *B. lepidus* (Figs 330, 331, 333, 334), *B. biroi* (Figs 338 & 339) and *B. rufofasciatus* (Figs 431–436, 438, 439) that occur with them, although the yellow pubescence is on tergum I for *B. himalayanus* and on tergum II for the other species. *B. himalayanus* is easily distinguished from all other species of the genus *Bombus* with similar colour patterns by using the subgeneric characteristics (see the key, couplets 1 & 2).

FOOD PLANTS. **Kashmir**: unidentified pink clover-like legume; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, unidentified dandelion-like composites; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Picrorhiza kurrooa* Royle ex Benth.; (Labiateae) *Thymus linearis* Benth. ex Benth.

Ladakh: (Leguminosae) *Caragana versicolor* (Wallich) Benth.

Bombus (Mendacibombus) marussinus Skorikov

(Figs 49, 89, 129, 169, 222, 254–257, Maps 9 & 10)

Bombus mendax subsp. *marussinus* Skorikov, 1910*a*: 330. Lectotype queen by designation of Podbolotskaya (in press), U.S.S.R.: Tadzhikistan S.S.R., Shugnan, 3000 m, 24–27.vi.1909 (*Makarjin*) (ZI) [examined].

Bombus (Mendacibombus) marussinus subsp. *afghanus* Reinig, 1940: 230. Syntype queen and male, presumed lost (Tkalců, 1969*a*, see also Note 4 on *B. biroi*), AFGHANISTAN: Badakhshan, Khwaja Muhammed, 3800–4000 m, 25.vii-10.viii.1936 (*Kotzsch*) [not seen]. **Syn. n.**

AFFINITIES. *B. marussinus* is closely similar to *B. himalayanus* and *B. turkestanicus* in morphology (Fig. 5, see the comments on *B. himalayanus*).

Female *B. marussinus* have fewer fine punctures on the labral ridge than do those of *B. himalayanus* (Figs 221 & 222) or *B. turkestanicus*. This difference appears to be retained in combination with the unbanded yellow thoracic dorsum where *B. marussinus* and *B. turkestanicus* occur together in the Tarest mountains of the Hindu Kush (BMNH) and where *B. marussinus* and *B. himalayanus* occur together in the Hindu Raj range (see the comments on *B. himalayanus*). I infer from this precise coincidence between the discontinuities in the patterns of variation, for both colour and sculpturing, that individuals of these three taxa are unlikely to be interbreeding. However, it is possible that there are narrow hybrid zones, so their specific status is still not certain. More information would be desirable concerning their mate-searching behaviour, where they occur together, in order to ascertain more directly whether or not they interbreed. The distribution of *B. turkestanicus* includes the Tien Shan (Skorikov, 1910*a*, 1931; Panfilov, 1957; ZI), the Pamir and the Hindu Kush ranges (BMNH). *B. turkestanicus* may occur in Kashmir, but I have yet to see specimens from this area that can be attributed definitely to this species (but cf. yellow workers assigned to *B. himalayanus*).

According to Tkalců (1969*a*), the syntypes of *B. marussinus* subsp. *afghanus* appear to have been lost. The original description contains nothing to distinguish this material from 'Chodja-Mahomed' [= Khwaja Muhammed] in the Hindu Kush from a slight variation of the colour pattern of the lectotype of *B. marussinus*. Tkalců ascribed material with a similar colour pattern from the 'Nachbargebiet Afghanistans (Karakorum)' to *B. afghanus* Reinig. From his detailed description and from an examination of a queen from Banidas kindly lent to me by Dr Tkalců, it is likely that these specimens from the Karakoram are part of the same species as the banded white *B. avinoviellus*, despite their uniformly yellow thoracic dorsa (see the comments on *B. avinoviellus*).

DISTRIBUTION. *B. marussinus* is a central Asian species (Map 9). It is known from the Hindu Kush (Reinig, 1940; Tkalců, 1969*a*; BMNH), the Pamir (Skorikov, 1910*a*; Reinig, 1930; Skorikov, 1931; ZI), Pakistan (PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. marussinus* has been recorded only from the Hindu Raj and western Karakoram ranges, in the drier subalpine scrub (Map 10): 5 queens, 7 workers, 2 males, from 5 localities 2700–3200 m (BMNH).

VARIATION WITHIN KASHMIR. All of the individuals of *B. marussinus* have some yellow hairs in the pubescence of terga I-II, although there is variation in the extent of this pale pubescence on tergum II (Figs 254–257). Workers have more pale pubescence ventrally, as for workers and queens of *B. turkestanicus*.

This species is closely similar in colour pattern to some of the *B. avinoviellus* (Fig. 232), *B. branickii* (Fig. 265), *B. subtypicus* (Figs 319–324), *B. biroi* (Fig. 335–337), *B. asiaticus* (Figs 371–376) and *B. semenovianus* (Figs 397–402) that may occur with it. It is, however, easily recognised using the subgeneric characteristics (see the key, couplets 1 & 2). *B. marussinus* can be separated from any *B. avinoviellus* with a similar colour pattern (Fig. 232) of the pubescence by its clear (hyaline) wings and by the specific characters (see the key, couplet 3).

FOOD PLANTS. No records.

Subgenus ***PSITHYRUS*** Lepeletier, **stat. n.**

Psithyrus Lepeletier, 1832: 373. Type species: *Apis rupestris* Fabricius, 1793: 320 = *Bombus rupestris* (Fabricius), by subsequent designation of Sandhouse (1943: 572).

Apathus Newman, 1835: 404 [footnote k]. Replacement name for *Psithyrus* Lepeletier, incorrectly stated to be a junior homonym of *Psithyros* Hubner (Lepidoptera).

Laboriopsithyrus Frison, 1927: 69 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Bombus laboriosus* Fabricius, 1804: 352 [?= *Emphoropsis laboriosa* (Fabricius)] in the sense of Frison [= *Bombus citrinus* (Smith), a misidentification, see Milliron (1960: 99), requiring designation by the ICZN (see Note below)] by original fixation. Provisional synonym.

Ashtonipsithyrus Frison, 1927: 69 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Apathus ashtoni* Cresson, 1864: 42 = *Bombus ashtoni* (Cresson), by original designation [p. 70]. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Fernaldaepsithyrus Frison, 1927: 70 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Psithyrus fernaldae* Franklin, 1911: 164 = *Bombus fernaldae* (Franklin), by original designation. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Eopsithyrus Popov, 1931: 134 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Apathus tibetanus* Morawitz, 1886: 202 = *Bombus tibetanus* (Morawitz), by original designation [p. 135]. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Metapsithyrus Popov, 1931: 135 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Apis campestris* Panzer, 1801: 74 = *Bombus campestris* (Panzer), by original designation. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Allopsithyrus Popov, 1931: 136 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Apis barbutella* Kirby, 1802: 343 = *Bombus barbutellus* (Kirby), by original designation. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Ceratopsithyrus Pittioni, 1949: 271 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Psithyrus klapperichi* Pittioni, 1949: 273 = *Bombus cornutus* (Frison) (see Tkalců, 1989), by original designation. Synonymised with *Psithyrus* Lepeletier by Milliron (1961).

Citrinopsithyrus Thorp [*in* Thorp *et al.*], 1983: 50 (as a subgenus of *Psithyrus* Lepeletier). Type species: *Apathus citrinus* Smith, 1854: 385 = *Bombus citrinus* (Smith), by original designation. **Syn. n.**

NOTE. Application of *Laboriopsithyrus* is a matter that should mandatorially be referred to the ICZN (Art. 70b). Since this name is treated here as a synonym of *Psithyrus*, I intend to take no action.

Descriptions of the diagnostic characters of both sexes for species of this subgenus are provided in the keys (couplet 1 for the females and couplet 2 for the males; for further details see Popov, 1931; Løken, 1984).

The many separate subgeneric names for species-groups of parasitic bumble bees are not used here, because the male genitalia of their type species are more similar to one another than is general among the subgenera of the genus *Bombus* (e.g. Pittioni, 1939*a*; Ito, 1985; Williams, 1985).

Knowledge of the systematics of species of the subgenus *Psithyrus* from Asia has been limited by the scarcity of material in collections. These bees are permanent social parasites in colonies of other species of the genus *Bombus* (e.g. reviews by Alford, 1975; Fisher, 1987; no records from colonies of species of the subgenus *Mendacibombus*). Consequently they are usually much less abundant than individuals of the host species. Many of the nominal taxa have been described from very small samples, collected at widely separated localities. There is therefore relatively little information available to describe the variation of many of the nominal taxa from Asia.

Bombus (Psithyrus) bohemicus Seidl

(Figs 21, 50, 90, 130, 170, 206, 258, Maps 11 & 12)

Apis nemorum Fabricius, 1775: 380. Lectotype female by designation of Løken (1984: 8) (see Note 1 below), DENMARK: Copenhagen, no further data (BMNH) [examined]. Junior primary homonym of *Apis nemorum* Scopoli, 1763.

Bombus bohemicus Seidl, 1837: 73. Type not found (Tkalců, 1969*b*) (see Note 2 below), CZECHOSLOVAKIA: Prague, no further data [not seen]. Synonymy with *Apis nemorum* Fabricius suggested by Blüthgen (1918), confirmed here.

TYPE MATERIAL. Note 1. In her revision of the Scandinavian *Psithyrus* fauna, Løken (1984) states that the 'type' of *Apis nemorum* F. is a female in the Banks collection (BMNH). This had been examined for her by I. H. H. Yarrow, who had ascribed it to the subgenus *Ashtonipsithyrus*. In this collection, above an original, handwritten drawer label that begins 'Apis nemorum ?', stand two female *Psithyrus* that carry Yarrow's determination labels. One is a female labelled *Psithyrus sylvestris* Lepeletier and the other a female labelled *Psithyrus bohemicus* by Yarrow, identifications that I confirm. Løken's use of the word 'type' in reference to the second specimen, which has had terga and sterna V-VI mounted on card on a separate pin, is taken to be a valid lectotype designation (Art. 74b).

Note 2. There is no reason to doubt the usual interpretation of *B. bohemicus*, so it is neither necessary nor valid to designate a neotype (Art. 75b).

AFFINITIES. The rare Mongolian (NMP) and Siberian (BMNH) *B. (Exilobombus) exil* (Skorikov) (justified emendation of '*Mucidobombus exiln. nov.*' Skorikov by Milliron, 1961: 56) shares a pronounced interio- basal process of the male gonostylus (Fig. 5) with all groups of bumble bees (synapomorphy), apart from the species of the subgenus *Mendacibombus* (secondarily partly reduced for species of the subgenera *Orientalibombus*, *Kallobombus* Dalla Torre, *Alpinobombus* Skorikov, *Pyrobombus* and *Cullumanobombus* Vogt). A general dorso-ventral flattening of the male gonostylus against the dorsal surface of the volsella is shared by most groups of bumble bees (?synapomorphy), apart from species of the subgenera *Mendacibombus*, *Exilobombus* Skorikov, *Confusibombus* and possibly *Bombias* (but see the comments on the subgenus *Mendacibombus*). The absence of an interio-apical process on the volsella is also shared by species of the subgenera *Eversmannibombus* and *Psithyrus* (possibly not a symplesiomorphy with *Mendacibombus*, see Williams 1985, but a secondary reduction and synapomorphy of *Eversmannibombus* + *Psithyrus*, Figs 130–132). The species of the subgenus *Psithyrus* share the development of a particularly dense brush of long, branched hairs associated with the interio-basal process of the male gonostylus (synapomorphy).

Within the subgenus *Psithyrus*, *B. bohemicus* belongs to a group of species (the *ashtoni*-group, formerly subgenus *Ashtonipsithyrus*) that share a reduction of the ventro-basal angle of the penis valve (Fig. 90) (synapomorphy). Most females of this group have the keels of sternum VI broad, narrowing apically where they converge before the apex of the sternum (Fig. 206) (the keels are more pronounced and blade-like in the North American *B. suckleyi* Greene).

Within the *ashtoni*-group, *B. bohemicus* shares with the North American (BMNH, PW) *B. ashtoni* (Cresson) and the Korean (Kim & Ito, 1987; BMNH) *B. coreanus* (Yasumatsu) the development of a pronounced shoulder on the outer side of the penis valve shaft, immediately behind the penis valve head (Fig. 50) (?synapomorphy). This shoulder is weakly developed in the European and North African (Popov, 1927*a*, 1931; Løken, 1984; BMNH, PW) *B. vestalis* (Geoffroy in Fourcroy), which can also be distinguished by its broader male gonostylus. The male of *B. coreanus* has the head of the penis valve shorter so that it is almost semi-circular in dorsal aspect, with the apex inwardly directed.

B. bohemicus is closely similar to the North American *B. ashtoni* and it is possible that they are parts of the same species. However, subtle differences in shape and sculpturing could be taken to reflect a lack of interbreeding as separate species. These differences include the broader male gonostylus, relative to the apex of the gonocoxite, and a slightly smaller ventro-basal angle of the penis valve for *B. ashtoni*.

DISTRIBUTION. *B. bohemicus* is one of the most widespread of all socially parasitic bumble bee species (Map 11). It is known from Europe (e.g. Popov, 1927*a*, 1931; Alford, 1975; Løken, 1984; BMNH, PW), south-eastwards to Turkey and the Caucasus (BMNH), and north-eastwards across the U.S.S.R. (Popov, 1927*a*, 1931; BMNH) to Kamchatka (Popov, 1927*a*; Bischoff, 1930). In central Asia it reaches southwards to the Tien Shan (Popov, 1927*a*, 1931), the Pamir (Popov, 1931) and Kashmir; and in the far east it reaches southwards to Mongolia (Popov, 1927*a*, 1931; Tkalců, 1974*a*; BMNH, PW), Inner Mongolia (Reinig, 1936), Heilongjiang (Popov, 1931), North Korea (Kim & Ito, 1987), Shanxi (Maa, 1948), Gansu (Bischoff, 1936) and Sichuan (Popov, 1927*a*).

MATERIAL EXAMINED FROM KASHMIR. *B. bohemicus* has been collected in Kashmir only at Lal Pani (Map 12): 10 males, 3000–3700 m, 2–3.ix.1953 (*Schmid*) (BMNH).

In Britain this species is known to breed in the nests of *B. lucorum* (Alford, 1975; see the comments on *B. lucorum*).

VARIATION WITHIN KASHMIR. The males from Kashmir are closely similar in colour pattern (Fig. 258) to individuals from Britain. Among the fauna of Kashmir, they are most similar to some males of *B. morawitzianus* (Fig. 270), but are easily distinguished by the narrow volsella. The females are likely to have a similar colour pattern to the males, but with very much less of the yellow pubescence at the rear of the thorax and on tergum I. This pattern is quite distinctive among the Kashmir fauna.

FOOD PLANTS. No records.

Bombus (Psithyrus) novus (Frison), comb. n.

(Figs 24, 28, 32, 36, 51, 91, 131, 171, 207, 259–262, Maps 13 & 14)

Psithyrus (Psithyrus) novus Frison, 1933: 340. Holotype female by original designation [p.

341], INDIA: Kashmir, Nagaberan, 10000–10500 ft [3000–3200 m] (*Bion*) (Calcutta) [not seen].

Psithyrus (Psithyrus) novus subsp. *nepalensis* Tkalců, 1974*b*: 318. Holotype female by original designation, NEPAL: Khumbu, Pheriche, 4300 m, 5.vii.1964 (*Dierl*) (ZS) [examined]. Provisional synonym.

AFFINITIES. *B. novus* belongs to a group of species (the *rupestris*-group, formerly subgenus *Psithyrus* s.str.) for which the volsella has an acutely produced inner corner (Figs 131 & 132) (synapomorphy). Females of this group have the keels of sternum VI blade-like and converging close to the apex of the sternum (Figs 207 & 208). The females have the mandibles conspicuously narrowed in the distal half (Fig. 32).

Within the *rupestris*-group, males of *B. rupestris* and *B. branickii* (see the comments on *B. branickii*) are distinguished by a slight elongation of the penis valve shaft between the penis valve head and the ventro-basal angle (Figs 51 & 52) and by the narrower distal part of the volsella (Figs 131 & 132) (?synapomorphies). The females have the clypeus closely and coarsely punctured almost throughout.

In contrast, other material from Kashmir runs to the name *Psithyrus morawitzi* Friese in Popov's (1931) key, although it agrees closely with the more recent description of *B. novus*. Tkalců (1974*b*) considered *B. novus* to belong to the '*chinensis*-Gruppe von *Psithyrus* s. str.'. From Popov's key this includes *B. chinensis* (Morawitz) and *B. morawitzi*, which were both described from Chinese material (from Gansu & Sichuan respectively). I have seen no specimens of either of these nominal taxa for comparison with *B. novus*. Bischoff (1936) also described material belonging to this group from Sichuan and Yunnan. His material showed the colour patterns both with and without yellow bands, as described for *B. chinensis* and *B. morawitzi* respectively, although he found that these individuals scarcely differed in morphology ('Morphologisch ist diese Form [*Psithyrus chinensis* subsp. *hoenei* Bischoff, with yellow pubescence] kaum von dem typischen *chinensis* zu trennen, weicht aber in der Färbung sehr stark ab.') and Bischoff identified them all as *Psithyrus chinensis*. More recently, Tkalců (1987) has regarded *Psithyrus morawitzi* as a subspecies of *Psithyrus chinensis*.

The holotype of *Psithyrus novus* subsp. *nepalensis* differs from *B. novus* s.str. not only in colour (which could be due in part to the fading of any yellow or orange pubescence to whitish for this abraded, old specimen), but also in several morphological details. In particular, none of the specimens from Kashmir has the basal keel of the mandible reaching the margin (Fig. 32, including the holotype, see Frison, 1933: fig. 5b). The weak incision in this part of the margin is present for the specimen from Nepal, as noted by Tkalců, but is not at all distinct for the specimens from Kashmir. The dorsal surface of the labral tubercles of the Nepalese specimen has many large punctures, which are few or lacking for the specimens from Kashmir. The unpunctured part of the ocello-ocular area extends nearly three-quarters of the breadth of the ocello-ocular distance for the specimen from Nepal but no more than half of the distance for the specimens from Kashmir. The weakly-arched transverse ridge of sternum II shows a median anterior deviation for the specimens from Kashmir that is not marked for the specimen from Nepal. However, both nominal taxa share a reduction in the density of the punctures on the clypeus and on antennal segment 1 (scape). With so little material available from the eastern Himalaya and from the intervening areas, especially of the males, I consider it premature to conclude that these nominal taxa represent separate species. More material is needed to establish the relationships of all of the nominal taxa in this group.

DISTRIBUTION. The present, provisional concept of *B. novus* is of a Himalayan species (Map 13). It is known from Nepal (Tkalců, 1974*b*; ZS), Himachal Pradesh (BMNH, PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. novus* is recorded from the southern side of the Great Himalaya range and from the Pir Panjal range, in mesic subalpine scrub (Map 14): 13 females, 31 males, from 2 localities 3000–3700 m (BMNH, BT, NR, PW).

During July and August 1986, I saw many females investigate gaps among large boulders that were lying in gullies in the subalpine zone of Mt Apharwat. Queens of several species of bumble bees had been seen at this site, many apparently searching for nest sites. Most abundant among these bees were queens of *B. rufofasciatus*.

VARIATION WITHIN KASHMIR. The colour pattern of only one of the females agrees closely with the original description, in that it has a broad black band between the wing bases (Fig. 261). Other females have only a few black hairs along the posterior margin of the scutum (Fig. 259). The putative males are associated with these females because, among material from Kashmir, they also belong to the *rupestris*-group but, unlike *B. branickii*, resemble female *B. novus* in having some form of black band between the wing bases (Figs 260 & 262). The males differ from the females in that the pale pubescence of the thorax and tergum I is grey-white, as for the female from Nepal (Tkalců, 1974*b*).

The colour pattern of the pubescence of the males is black, with the sides of the thorax as far as the leg bases, the rather poorly-defined anterior and posterior bands on the thoracic dorsum and tergum I grey-white; terga II-III pale yellow; terga IV-VII orange-red, with variable degrees of replacement by black basally on tergum IV (Fig. 260), which may extend over the entire tergum (Fig. 262); sterna and legs predominantly black. The wings are weakly to moderately strongly clouded with brown (infuscated).

The colour pattern of the males (Figs 260 & 262) is similar to that of some males of *B. himalayanus* (Figs 246, 249, 252), *B. kashmirensis* (Fig. 304), *B. rufofasciatus* (Figs 433, 436, 439), and probably *B. lemniscatus* (cf. Figs 325 & 326), that occur in the same localities.

FOOD PLANTS. (Ranunculaceae) *Aconitum laeve* Royle; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Scrophularia pauciflora* Benth.

Bombus (Psithyrus) branickii (Radoszkowski), comb. n.

(Figs 52, 92, 132, 172, 208, 263–266, Maps 15 & 16)

Psithyrus Branickii Radoszkowski, 1893: 241. Lectotype female by designation of Tkalců (1969*a*: 204), U.S.S.R.: ?Kirgiziya S.S.R., 'Kara-Karyk' mountains, 10000 ft [3000 m] (*Barei*) (MNHU) [examined].

Psithyrus rupestris var. *eriophoroides* Reinig, 1930: 110 (see Note 1 below). 4 syntype males, U.S.S.R.: Tadzhikistan S.S.R.; Kirgiziya S.S.R.; CHINA: Xinjiang (ITZ) [not seen]. Synonymised with *Psithyrus branickii* Radoszkowski by Tkalců (1969*a*).

Psithyrus (Psithyrus) rupestris subsp. *elisabethae* Reinig, 1940: 231. Holotype female by monotypy (see Note 2 below), AFGHANISTAN: Hindu Kush, north side of 'Nuksan' pass, 3500–4000 m, mid vii.1936 (*Kotzsch*) (ZS) [examined]. Synonymised with *Psithyrus branickii* Radoszkowski by Tkalců (1969*a*).

NOMENCLATURE. Note 1. Reinig's use (1930: 83 etc.) of the term 'ssp.' elsewhere in his paper is taken to indicate that infrasubspecific rank is meant for *Psithyrus rupestris* var. *eriophoroides*. However, this name has subsequently been treated as a name in the species group by Reinig (1935), so it is deemed to be of subspecific rank (Art. 45g(ii)(1)).

TYPE MATERIAL. Note 2. Reinig's description of *Psithyrus rupestris* subsp. *elisabethae* specifies that only a single female was examined. A single female in the ZS collection agrees with the original description and bears labels with the data quoted. It also bears a red typed label 'Holotypus' and a handwritten label 'Psithyrus (Ps.) / rupestris Fabr. / ssp. elisabethae / [female] n. Reinig / det.W.F.Reinig 1939'. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. *B. branickii* belongs to the *rupestris*-group and is closely similar to *B. rupestris* (see the comments on *B. novus*), a Eurosiberian species (e.g. Popov, 1931; Reinig, 1935; Løken, 1984). *B. rupestris* is known from an area that reaches south-eastwards from Europe to Turkey and the Caucasus (BMNH); in central Asia it reaches south to the Altai (Popov, 1931); and in the far east it reaches southwards to Mongolia (Popov, 1931; Tkalců, 1974*a*; BMNH), Inner Mongolia (Reinig, 1936), and Gansu (Popov, 1931; Bischoff, 1936). *B. branickii* has shallower and less well-defined post-ocular punctures, has a weaker post-ocular groove on the vertex (the 'dorsal furrow of the gena' in Richards, 1968) and has longer pubescence. This is especially evident in the posterior fringe of the hind basitarsus, where the length of the hairs exceeds the breadth of the basitarsus for *B. branickii*, but not for *B. rupestris*. The wings of *B. branickii* are also only moderately, rather than very strongly, darkened (infuscated).

DISTRIBUTION. *B. branickii* is a central Asian and Tibetan species from the mountains around the deserts of China (Map 15). It is known from Transbaikal, Mongolia and the Altai (Popov, 1931), the Tien Shan (Radoszkowski, 1893; Morawitz, 1894; Popov, 1931; Maa, 1948; MNHU), the Pamir (Reinig, 1930), the Hindu Kush (Reinig, 1940; Tkalců, 1969*a*; BMNH, ZS), Kashmir, Himachal Pradesh (BMNH, PW), Tibet (BMNH), Sichuan (Reinig, 1935), Shanxi (Yasumatsu, 1951) and North Korea (Kim & Ito, 1987). Reinig (1935: chart 1) mapped part of this distribution under the name *Psithyrus rupestris* subsp. *eriophoroides*.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. branickii* is recorded from the Hindu Raj, Great Himalaya and Zanskar ranges, in the drier alpine scrub and steppe (Map 16): 21 females, 71 males, from 9 localities 1500–4800 m (BMNH, IZ, MI, NM, PW).

During July 1980, I saw females of this species investigate gaps under boulders and holes in dry-stone walls on Nimaling plain. Although queens of 8 species of the genus *Bombus* were flying in the area, only *B. asiaticus*, *B. kashmirensis* and *B. keriensis* had workers flying at this time.

VARIATION WITHIN KASHMIR. One of the females from Atro Sar (Fig. 266) and another from Sonamarg agree closely in colour pattern with the original description, in that the pubescence of terga V-VI is entirely black. The remaining females have red pubescence on these terga (Figs 263, 265). All females have tergum I yellow and often have a few pale hairs apico-laterally on tergum II. Two females from Nimaling have more of these pale hairs on tergum II, so as to form an apical band that is only interrupted in the middle by black. Another two females from the same locality also have a pale, apical band on tergum III (Fig. 263). The males associated with these females belong to the *rupestris*-group, but unlike *B. novus*, they lack a black band in the pubescence between the wing bases, although they do have a few black hairs intermixed on the thoracic dorsum (Fig. 264).

Some individuals (Fig. 265) are closely similar in colour pattern to some *B. avinoviellus* (Fig. 232), *B. marussinus* (Figs 254–257), *B. subtypicus* (Figs 319–324), *B. biroi* (Figs 335–337), *B. asiaticus* (Figs 371–376) and *B. semenovianus* (Figs 397–402) that may occur with them. *B. branickii* is easily distinguished by the subgeneric characters (see the key, couplets 1 & 2).

FOOD PLANTS. (Leguminosae) *Caragana versicolor* (Wallich) ex Benth.; unidentified yellow thistle-like composites.

Bombus (Psithyrus) ferganicus (Radoszkowski), **comb. n.**

(Figs 22, 53, 93, 133, 173, 209, 267, 268, Maps 17 & 18)

Psithyrus ferganicus Radoszkowski, 1893: 241. Lectotype female by designation of Tkalců (1969*a*: 206), U.S.S.R.: ?Kirgiziya S.S.R., 'Kara-Karyk' mountains (MNHU) [examined].

Psithyrus indicus Richards, 1929*a*: 139. Holotype male by original designation [p. 141], INDIA: Kashmir, Gulmarg, 1913 (*Thomson*) (BMNH) [examined]. Synonymised with *Psithyrus ferganicus* Radoszkowski by Grütte (1937).

AFFINITIES. *B. ferganicus* belongs to a group of species (the *campestris*-group, formerly subgenus *Metapsithyrus*) for which the apical part of the volsella is greatly broadened (Figs 133 & 134) and the ventro-basal angle of the penis valve is apically rounded, although this angle retains its curved, hook-like form (Figs 53 & 54) (synapomorphies). Females of this group have the keels of sternum VI broad throughout their length, although they converge distinctly before and below the apex of the sternum (Figs 209 & 210).

Within the *campestris*-group, *B. ferganicus* shows the least broadening of the volsella (Figs 133 & 134) (see the comments on *B. morawitzianus*). The most similar European species is the Euro-siberian (e.g. Popov, 1931; Alford, 1975; Løken, 1984) *B. campestris* (Panzer). From Europe *B. campestris* reaches south-eastwards to Turkey (BMNH), the Caucasus (Popov, 1931; BMNH) and the Elburz (BMNH); from central Asia it reaches southwards to the Tien Shan (Popov, 1931); and in the far east it reaches southwards to Mongolia (Popov, 1931; Tkalců, 1974*a*; BMNH), Inner Mongolia (Reinig, 1936), Ningxia (Popov, 1931), and Gansu (Popov, 1931; Bischoff, 1936). The unique female of *B. susteraianus* (Tkalců) from North Korea is closely similar to *B. campestris*, but has slightly less pronounced keels of sternum VI (Tkalců, 1959) and slightly more pronounced labral tubercles. The male of this nominal taxon remains unknown. The Chinese *B. pieli* (Maa) (synonymised with *Psithyrus tajushanensis* Pittioni by Tkalců, 1987) is known from Sichuan (Tkalců, 1987; BMNH), Hubei (Sakagami, 1972), Anhui and Zheijiang (Maa, 1948) and Fujian (Pittioni, 1949; Tkalců, 1987; BMNH). The male genitalia of *B. ferganicus*, in ventral aspect, have the distal half of the volsella narrower than for *B. campestris* or *B. morawitzianus*. I have not seen males of *B. pieli*, but Maa (1948: fig. 16) described its volsella as slightly shorter than for *B. campestris*. Females of *B. ferganicus* can be distinguished from those of the other three species by the shallower punctures of the post-ocular area. These punctures are widely spaced for *B. ferganicus*, as for *B. morawitzianus*, but in contrast they are very shallow and poorly-defined, so that the area is nearly smooth and strongly shining. The females of *B. campestris* and *B. pieli* have smaller punctures in the post-ocular area, separated by less than their own widths, though these punctures are slightly closer and better defined for *B. pieli*. *B. pieli* can also be distinguished from *B. campestris* by their labral tubercles, which are more strongly angled.

DISTRIBUTION. *B. ferganicus* is a central Asian species (Map 17). It is known from the Tien Shan (Radoszkowski, 1893; Morawitz, 1894; Grütte, 1937; MNHU), the Hindu Kush (Reinig, 1937;

Tkalců, 1969*a*; BMNH, PW), Pakistan (PW), Kashmir and Himachal Pradesh (BMNH, PW).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. ferganicus* is recorded from the western Karakoram, Great Himalaya and Pir Panjal ranges, in both montane coniferous forest and subalpine scrub (Map 18): 14 females, 115 males, from 5 localities 2400–3700 m (BMNH, BT, NR, PW, ZM, ZS).

VARIATION WITHIN KASHMIR. Only minor variation is evident in the replacement of pale hair on the gaster by black, especially on terga I-II, and in the colour of the pale hair, which varies from lemon-yellow to brown (Figs 267 & 268). This species is quite distinctive in colour pattern among the fauna of Kashmir.

FOOD PLANTS. (Leguminosae) *Trifolium repens* L.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC.

Bombus (Psithyrus) morawitzianus (Popov), **comb. n.**

(Figs 54, 94, 134, 174, 210, 269, 270, Maps 19 & 20)

Psithyrus (Metapsithyrus) morawitzianus Popov, 1931: 148, 183 (see Note 1 below). Lectotype female by designation of Podbolotskaya (in press), U.S.S.R.: Kirgiziya S.S.R., Naryn, 19. vii.1904[?] (ZI) [examined].

Psithyrus (Metapsithyrus) redikorzevi Popov, 1931: 160, 181. 5 syntype males, U.S.S.R.: Tadzhikistan S.S.R.; Kirgiziya S.S.R. (ZI) [not seen]. Synonymised with *Psithyrus morawitzianus* Popov by Grütte (1937) (see Note 2 below).

NOMENCLATURE. Note 1. Popov described *Psithyrus morawitzianus* with particular reference to a female that bore Vogt's manuscript label '*Ps. campestris* var. *morawitzianus* typicus O.V. Cotype' (Popov, 1931: 183, although the label actually reads '*Ps. campestris* / var. *morawitzianus* O.V. / typicus O.V. / Cotype'). Therefore Popov is deemed to be the author (Art. 50a).

Note 2. Following the Principle of the First Reviser (Art. 24), *B. morawitzianus* is accepted in precedence to *B. redikorzevi*, by the action of Grütte (1937).

AFFINITIES. *B. morawitzianus*, like *B. ferganicus*, belongs to the *campestris*-group (see the comments on *B. ferganicus*). The male genitalia of *B. morawitzianus* clearly differ from those of *B. ferganicus*, *B. campestris* and *B. pieli* by the great breadth of the distal half of the volsella, in ventral aspect (Figs 133 & 134), and by the extremely short, or transverse, gonostylus (Figs 173 & 174). The punctures of the post-ocular area of the female *B. morawitzianus* are larger, more distinct and more widely spaced than for individuals of *B. ferganicus*, *B. campestris* or *B. pieli*. The punctures of tergum VI are finer for *B. morawitzianus* than for individuals of *B. ferganicus*, *B. campestris* or *B. pieli*.

DISTRIBUTION. *B. morawitzianus* is a central Asian species (Map 19). It is known from the Tien Shan (Morawitz, 1875; Popov, 1931; Grütte, 1937; ZI), the Pamir (Popov, 1931; Grütte, 1937), the Hindu Kush (Reinig, 1940; Tkalců, 1969*a*) and Kashmir. A record from the Kopet Dag (Rasmont, 1983*b*) needs to be confirmed.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. morawitzianus* is recorded from the Hindu Raj and Great Himalaya ranges (Map 20): 1 female, 7 males, from 4 localities 2700–4000 m (BMNH).

VARIATION WITHIN KASHMIR. The colour patterns of both sexes are similar to those described by Popov (1931) (Figs 269 & 270). There is some variation in the colour of the pale pubescence of the male gaster between white and dull yellow. This species is quite distinctive in colour pattern among the fauna of Kashmir.

FOOD PLANTS. No records.

Bombus (Psithyrus) skorikovi (Popov), **comb. n.**

(Figs 55, 95, 135, 175, 211, 271–274, Maps 21 & 22)

Psithyrus skorikovi Popov, 1927*b*: 267. Holotype female by original designation [p. 268], CHINA: Gansu [?or Qinghai], northern slopes of the Xining mountains, before 1.vii.1910 (*Grum-Grzhimailo*) (ZI) [examined].

[*Psithyrus skorikovi* var. *mesoxanthus* Richards, 1928*c*: 360 [examined]. Infrasubspecific (see Note 1 below) (Art 45g(ii)(1)), unavailable name (Art. 45e).]

Psithyrus (Fernaldaepsithyrus) gansuensis Popov, 1931: 168, 202. Holotype male by monotypy (see Note 2 below), CHINA: Qinghai, 'Ui-ju' to 'Choto', 15–16.viii.1908 (*Kozlov*) (ZI) [not seen]. Synonymy with *Psithyrus skorikovi* suggested by Popov (1931), confirmed here.

NOMENCLATURE. Note 1. In the introduction to his paper, Richards (1928*c*: 345) contrasts his use of the term 'varieties', for 'sporadically' occurring colour variations, with the term 'races', which he used for '. . . *populations* inhabiting definite, usually continuous, areas and characterised by peculiarities of sculpture, hair-length or average colour-pattern.'. This is taken to show that infrasubspecific rank is meant for *Psithyrus skorikovi* var. *mesoxanthus*.

TYPE MATERIAL. Note 2. Popov's description of *Psithyrus gansuensis* specifies that only a single male was examined. If only a single male with the data quoted can be found, then this specimen should be regarded as the holotype (Art. 73a(ii)).

AFFINITIES. *B. skorikovi* belongs to a group of morphologically similar species (the *fernaldae*-group, formerly subgenus *Fernaldaepsithyrus*) of mainly Eurosiberian distribution (e.g. Popov, 1931; Løken, 1984), with one North American species (*B. fernaldae* (Franklin)). These species share a great reduction in the breadth of the male volsella (Fig. 135) and a narrowing of the apex of the gonocoxite (synapomorphies). Females of this group have the keels of sternum VI narrowed apically and converging a long way before the apex of the sternum (Fig. 211). This apex is itself narrowed into a ventrally-curved spine, which projects distinctly beyond the apex of tergum VI.

Within the *fernaldae*-group, *B. skorikovi* is most similar to the Eurosiberian (e.g. Popov, 1931; Løken, 1984) *B. flavidus* Eversmann in that the ventro-basal angle of the penis valve remains acute and strongly hook-shaped (Figs 55 & 95). *B. flavidus* is otherwise unique within the *fernaldae*-group for its restricted distribution in the subalpine and subarctic zones (see Pittioni, 1942: map 4; Løken, 1984). In southern Europe, *B. flavidus* is known from the Pyrenees, the Alps and western Turkey (Pittioni, 1942; BMNH). In a separate northern area of distribution it reaches eastwards from Scandinavia to Kamchatka (Popov, 1931; Pittioni, 1942), without records from further south than Lake Baikal. The females of *B. skorikovi* differ from those of *B. flavidus* in the weaker basal keel of the mandible, in the less extensively and less densely punctured ocello-ocular area and in the more strongly marked labral tubercles and lamella. The male of *B. skorikovi* has the ventro-basal angle of the penis valve much narrower. The single male from Qinghai described by Popov under the name *Psithyrus gansuensis* appears from the description of the penis valve (see Popov, 1931: fig. 26D) to be a male of *B. skorikovi*. A single female from Qinghai described by Tkalců (1961) under the name *Psithyrus kuani* also appears to be closely similar to *B. skorikovi*. I have not seen either of these specimens.

The females from Kashmir that are ascribed here to *B. skorikovi* differ from specimens from Qinghai and Gansu in that tergum VI has, at most, only a very weak median ridge and there are more large punctures with fewer small punctures. For some of the females from Kashmir the sculpturing of the surface of tergum VI is weaker so that it appears more strongly shining. However, some of the females from southern Tibet appear to be intermediate, at least in the reduction of the median ridge (Richards, 1928*c*; BMNH). It is considered premature to regard the Kashmir material as part of a separate species.

DISTRIBUTION. *B. skorikovi* is a peri-Tibetan species (Map 21). It is known from Kashmir, southern Tibet (Richards, 1928*c*; BMNH), Qinghai (Popov, 1931; Tkalců, 1961; ZS) and Gansu (Popov, 1927*b*, 1931; Bischoff, 1936; PW, ZI).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. skorikovi* is recorded from the southern side of the Great Himalaya range and from the Pir Panjal range (Map 22): 15 females, 301 males, from 2 localities 2700–3700 m (BMNH, NR, PW).

VARIATION WITHIN KASHMIR. Females from Mt Apharwat are similar in colour pattern to the holotype, although the apical margin of tergum II is yellow, whereas the median part of tergum IV and the entirety of tergum V are black-haired (Fig. 273).

The majority of the females from Lal Pani have the black pubescence of the thoracic dorsum reduced to a small, indistinct patch at the rear of the scutum and have more yellow hairs on the lateral parts of terga II and IV (Fig. 271). The putative males are associated with these females because they are the only males of the *fernaldae*-group of species among the material from Kashmir and occur together with the known females at Lal Pani, in the Kishanganga valley.

The colour pattern of the pubescence of the male (Figs 272 & 274) is dull yellow, except for black on the front and sides of the head, in a poorly-defined band between the wing bases, on terga V-VII and as a very few hairs in the middle of the posterior margin of tergum IV; the dark hairs of terga VI-VII are pale-tipped and often distinctly orange; the hairs of the legs are predominantly black, with some pale hairs intermixed. The wings are weakly clouded with brown (infuscated). Some males have the black band between the wing bases much reduced (120/301 males) (Fig. 272), as described for the female. A few males have a strong admixture of black hairs basally on tergum II (25/301 males, Fig. 274).

This species is quite distinctive in colour pattern among the fauna of Kashmir.

FOOD PLANTS. (Compositae) *Cirsium falconeri* (Hook.f.) Petrak; (Scrophulariaceae) *Scrophularia pauciflora* Benth.

Subgenus ***DIVERSOBOMBUS*** Skorikov

Diversobombus Skorikov, 1914*d*: 406 (as a subgenus of *Bombus* Latreille). Type species: *Bombus diversus* Smith, 1869: 207, by subsequent designation of Sandhouse (1943: 546).

Diversibombus Skorikov; Skorikov, 1938*b*: 1. Unjustified emendation (Art. 33b(i, iii)).

For a general description of both sexes see Richards (1968).

Bombus (Diversobombus) trifasciatus Smith

(Figs 11, 17, 39, 56, 96, 136, 176, 275–278, Maps 23 & 24)

Bombus trifasciatus Smith, 1852*a*: 43. LECTOTYPE queen by present designation (see Note 1 below), CHINA: Zhejiang, Zhoushan (*Fortune*) (BMNH) [examined].

Bombus montivagus Smith, 1878*b*: 168 [posthumous re-proposal in error, 1879: 131]. Lectotype queen by designation of Tkalců (1968*b*: 23), BURMA: Karen, Moolaiyet, 3000–6000 ft [900–1800 m] (BMNH) [examined]. **Syn. n.**

Bombus secundus Dalla Torre, 1890: 139. Replacement name for *Bombus montivagus* Smith, 1879, junior primary homonym of *Bombus montivagus* Smith, 1878*b*. Synonymised with *Megabombus montivagus montivagus* (Smith, 1878*b*) by Tkalců (1968*b*). **Syn. n.**

Bombus ningpoënsis Friese, 1909: 676. 2 syntype workers, CHINA: Zhejiang, Ningbo (MNHU) [not seen]. Synonymised with *Bombus trifasciatus* Smith by Tkalců (1961).

Bombus wilemani Cockerell, 1911: 100. Holotype worker by original designation [p. 101], TAIWAN: Arizan, 7500 ft [2300 m], 11.ix.1906 (*Wileman*) (BMNH) [examined]. Provisional synonym.

Bombus haemorrhoidalis var. *albopleuralis* Friese, 1916: 108. Lectotype queen by designation of Tkalců (1974*b*: 344), INDIA: Uttar Pradesh, Kumaun, 21.vi.1910 (MNHU) [examined]. **Syn. n.**

Bombus maxwelli Pendlebury, 1923: 67. Holotype queen by monotypy (see Note 2 below), WEST MALAYSIA: Pahang, Gunong Berumbun, 4800 ft [1500 m], 4.ix.1922 (BMNH) [examined]. Provisional synonym.

Bombus (Hortobombus) mimeticus Richards, 1931: 529. Holotype queen by original designation [p. 530], INDIA: West Bengal, Darjiling, Tukvar, 4000 ft [1200 m], iv.1894 (*Bingham*) (BMNH) [examined]. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *albolateralis* Richards, 1931: 530. Holotype worker by monotypy (see Note 3 below), NEPAL: no further data (BMNH) [examined]. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *gantokiensis* Richards, 1931: 530. Holotype queen by monotypy (see Note 4 below), INDIA: Sikkim, Gantok, 24.vi.1903 (BMNH) [examined]. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *turneri* Richards, 1931: 530. LECTOTYPE queen by present designation (see Note 5 below), INDIA: Meghalaya, Shillong, v.1903 (*Turner*) (BMNH) [examined]. Junior secondary homonym in *Bombus* of *Psithyrus turneri* Richards, 1929*a* [= *B. turneri* (Richards)]. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *insidiosus* Richards, 1931: 531. Holotype queen by original designation, PAKISTAN: Baltistan, no further data (BMNH) [examined]. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *geminatus* Richards, 1931: 531. Holotype worker by monotypy (see Note 6 below), INDIA: Kashmir, Gulmarg, 1913 (*Thomson*) (BMNH) [examined]. Synonymised with *Megabombus albopleuralis albopleuralis* (Friese) by Tkalců, 1974b. **Syn. n.**

Bombus (Hortobombus) mimeticus var. *magrettianus* Richards, 1931: 531. Holotype male by original designation [p. 533], ?BURMA [not Sikkim (see Note 7 below)]: no further data (MNHU) [examined]. **Syn. n.**

Bombus (Diversobombus) ningpoensis subsp. *minshanicus* Bischoff, 1936: 19. LECTOTYPE worker by present designation (see Note 8 below), CHINA: Gansu/Sichuan border, 'Ma-tou-shan', 600–1000 m, 2.vi.1930 (*Hummel*) (MNHU) [examined]. **Syn. n.**

Megabombus (Diversobombus) montivagus subsp. *quasibreviceps* Tkalců, 1968*b*: 27. Holotype queen by original designation, CHINA: Yunnan, no further data (Genf) [not seen]. **Syn. n.**

Megabombus (Diversobombus) albopleuralis subsp. *atropygus* Tkalců, 1989: 58. Holotype worker by original designation, BURMA: Nam Tamai valley, 27°48′N 97°48′E, 3500 ft [1067 m], 12.ix.1938 (*Kaulback*) (BMNH) [examined]. **Syn. n.**

TYPE MATERIAL. Note 1. There are two queens of *B. trifasciatus* in the BMNH collection labelled 'Shang / hai' that may have been among Smith's syntypes in 1852. The original description quotes neighbouring 'Chusan' [= Zhoushan] as the type-locality. Much of Fortune's material is labelled 'Shang / hai', although Smith described it as from 'Chusan' on Fortune's advice (Smith, 1852*a*: 33, 43), even when some of it must have originated from India (see the comments on *B. haemorrhoidalis*). In this case there is no reason to doubt Zhoushan as the area of origin of the material. The queen that agrees most closely with the description, by the absence of a distinct black band between the wing bases, carries a purple-edged label (1) 'Lecto- / type'; (2) a blue label 'Shang / hai', reverse side '52 / 28'; (3) 'trifasciatus / Type Sm.', in handwriting identical to that of Smith; (4) '*Bombus / trifasciatus* / TYPE. Smith'; (5) a red-edged, printed label 'Type'; (6) 'B.M. TYPE / HYM. / 17B.1028.'. According to the accessions catalogue, the number 52/28 refers to 17 Hymenoptera collected at 'Shanghai' by Fortune and purchased from him between February 28th and March 6th, 1852, which predates the reading of Smith's paper at the meeting (3.v.1852) of the Entomological Society of London by two months. This specimen, which lacks both hind legs, the distal joints of all the remaining tarsi and part of the right antennal flagellum, is designated as lectotype (Art. 74a).

Note 2. Pendlebury stated that he had seen two specimens of *B. maxwelli*: a queen, which he described, and a 'similar' worker. The 'Type and paratype' were then said to have been deposited in the Federated Malay States Museum, Kuala Lumpur. A single pre-1923 queen in the BMNH agrees with the original description and bears labels with the data quoted by Pendlebury, together with a label 'Bombus / maxwelli Pendl. / Type. Pahang.' and an accession number 1926–167. This number refers to a collection that is specified to have included eight Hymenopteran types, which was presented to the BMNH from the museum at Kuala Lumpur in 1926. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 3. Richards's description of *B. mimeticus* var. *albolateralis* specifies that only one worker was examined. A single pre-1931 worker in the BMNH collection agrees with the original description and bears labels with the data quoted. It also carries a label with the name *B. mimeticus* var. *albolateralis* and 'TYPE', in handwriting identical to that of Richards. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 4. Richards's description of *B. mimeticus* var. *gantokiensis* specifies that only a single queen was examined. A single pre-1931 queen in the BMNH collection agrees with the original description and bears labels with the data quoted. It also carries a label with the name *B. mimeticus* var. *gantokiensis* and 'TYPE', in handwriting identical to that of Richards. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 5. The original description of *B. mimeticus* var. *turneri* lists one queen and one worker as typical. A single pre-1931 queen in the BMNH collection bears a purple-edged label (1) 'Lecto- / type'; (2) 'Assam / R. Turner. / 1905–175'; (3) '*Shillong* / 5.03'; (4) 'B. orientalis var.'; (5) 'B. MIMETICUS / RICHARDS / VAR. TURNERI / RICHARDS. / Type [female]' in handwriting identical to that of Richards; (6) a red-edged label 'Type'; (7) 'B.M. TYPE / HYM. / 17B.1027.'. This specimen, which lacks the distal tarsal joints of all legs, the tibia of the right mid leg, all of the right front leg and most of both antennal flagella, is designated as lectotype (Art. 74a).

Note 6. Richards's description of *B. mimeticus* var. *geminatus* lists two workers, the second of which is specified to be the paratype. A single pre-1931 worker in the BMNH collection agrees with the original description and bears labels with the data quoted for the first worker. It also carries a label with the name *B. mimeticus* var. *geminatus* and 'TYPE', in handwriting identical to that of Richards. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 7. Tkalců (1968*b*: 27) questioned the validity of the locality data 'Sikkim' associated with the holotype of *B. mimeticus* var. *magrettianus* Richards. The other material with this colour pattern that Tkalců had examined bears labels for 'Tenasserim' in Burma.

Note 8. Bischoff's description of *B. ningpoensis* subsp. *minshanicus* lists two workers from Gansu, dated '14.5' and '2.6'. A worker in the MNHU collection bears Bischoff's labels with this name, the date 14.5.1930 and a red label 'Para-/Typus'. A second worker in the MNHU collection agrees with the description and bears a printed label (1) 'Sven Hedins / Exp. Ctr. Asien / Dr *Hummel*'; (2) 'Kina / S. Kansu'; (3) 'ningpoensis / minshanicus / n. subsp. [worker] / det. Bischoff'; (4) '(Bombus) loubouen- / sis Friese m. minshani- / cus (Bisch.) / *Skorikov* det.'; (5) a red label '68 / 61'; (6) a pencilled label 'loubouensis Friese / var. nov.'; (7) a pencilled label '2/6'; (8) 'M. (D.) tri- / fasciatus (Sm. / Tkalců det.'; (9) 'Zool. Mus. / Berlin'. This second specimen, which lacks only the tarsi of the left mid leg, is designated as lectotype (Art. 74a).

AFFINITIES. The species of the subgenera *Megabombus* Dalla Torre, *Senexibombus* Frison and *Diversobombus* share a displacement of the two hooks on the inner margin of the volsella to a narrowly subapical position (Fig. 136), and the interio-basal process of the male gonostylus is extended as a strongly recurved cusp (Fig. 176) (synapomorphies). The species of the subgenus *Diversobombus* share an enlargement of the inner hooks of the volsella, of which the inner basal hook has become broadened and carries many small teeth (?synapomorphy).

Within the subgenus *Diversobombus*, two species-groups have been recognised, the *trifasciatus*-group and the *diversus*-group (Sakagami, 1972). Species of the *diversus*-group have the recurved part of the cuspate interio-basal process of the gonostylus reduced to a single, long, slender spine (?synapomorphy) (see Tkalců, 1965: figs 46 & 47). These species include the Japanese *B. diversus* Smith (distribution mapped by Sakagami, 1975: fig. 14; see also Ito, 1987), the Chinese *B. longipes* Friese (synonymised with *B. hummeli* Bischoff by Tkalců, 1987, and possibly also conspecific with *Diversobombus malaisei* Skorikov [not seen]) and the more widespread east Asian *B. ussurensis* Radoszkowski (distribution mapped by Sakagami, 1975: fig. 14).

For males of the *trifasciatus*-group, the recurved part of the cuspate interio-basal process of the gonostylus bifurcates near its base, so that it forms two shorter, strongly curved spines (Fig. 176) (?plesiomorphy within the subgenus *Diversobombus*). Females can be distinguished from those of the *diversus*-group by their well-defined punctures of the post ocello-ocular area, whereas these punctures are embedded in coarse sculpturing for the species of the *diversus*-group.

Three widespread nominal taxa have been recognised in the *trifasciatus*-group, which have been described under the names *B. trifasciatus* s.str., *B. montivagus* and *B. haemorrhoidalis* var. *albopleuralis*. They differ principally in colour pattern, possibly as members of regional groups of Müllerian mimics (Fig. 11, see the discussion of the colour patterns of the Kashmir fauna). These nominal taxa of the subgenus *Diversobombus* are very similar in colour pattern to the individuals of *B. (Orientalibombus) haemorrhoidalis*, *B. (Alpigenobombus) breviceps* Smith and *B. (Pyrobombus) rotundiceps* Friese that occur with them (see the comments on *B. haemorrhoidalis*, *B. kashmirensis* and *B. lemniscatus* respectively; Sakagami & Yoshikawa, 1961; Tkalců, 1968*b*, 1989).

B. haemorrhoidalis var. *albopleuralis* is the oldest available name for the Himalayan nominal taxa of the *trifasciatus*-group (the '*montivagus*-Gruppe' of Tkalců, 1974*b*), which were first described as a species separate from *B. haemorrhoidalis* by Richards (1931), under the name *B. mimeticus*. The colour pattern of the pubescence on the thoracic dorsum is usually entirely black. There is variation in the amount of grey-white pubescence on the sides of the thorax (pleura). This pale pubescence is most often extensive in males. Among the material examined in the BMNH, the highest proportions of individuals with extensively pale-haired pleura appear to be from localities at lower altitudes in the eastern Himalaya. The pubescence of gastral terga I-II is usually bright lemon-yellow. The remaining gastral terga III-VI are predominantly red for individuals from the western Himalaya to as far east as Nepal, although the same extensively red pattern is also shown by two workers labelled 'Manipur' (females with terga III-VI red and without the white pubescence on the thorax were described under the name *B. mimeticus* var. *insidiosus* by Richards, whereas he described similar workers with the white pubescence under the name *B. mimeticus* var. *geminatus*). The red pubescence is replaced by black on tergum III or even on tergum IV for individuals from eastern Nepal eastwards to Arunachal Pradesh (these females with more extensive black on terga III-VI and without the white pubescence on the thorax were described under the name *B. mimeticus* var. *gantokiensis* by Richards for those with terga I-II pale yellow, or *B. mimeticus* s.str. for those with terga I-II creamy-white; Richards described similar females with the white pubescence under the name *B. mimeticus* var. *turneri* for those with terga I-II pale yellow, or *B. mimeticus* var. *albolateralis* for those with terga I-II creamy-white). Further east, the pubescence of terga III-VI is entirely black for individuals from northern Burma (described under the name *Megabombus albopleuralis* subsp. *atropygus* by Tkalců, 1989).

Material from further south in the highlands of South East Asia was described under the name *B. montivagus* by Smith (1878*b*). These individuals usually have the pubescence of the thorax bright orange, often paler yellow or grey-white at the sides, with a black band between the wing bases. The pubescence of tergum I and of the base of tergum II is bright lemon-yellow. Some specimens from above Hanoi have gastral terga III-VI black (described under the name *Megabombus montivagus* subsp. *quasibreviceps* by Tkalců, 1968*b*), as for the north Burmese *Megabombus albopleuralis* subsp. *atropygus*, but individuals from most of South East Asia have red pubescence on the apical terga, as for the east Himalayan *B. haemorrhoidalis* var. *albopleuralis*.

Material from further to the north and east, in China, was described by Smith (1852*a*) under the name *B. trifasciatus* s.str. These individuals also have pale pubescence on the thorax and on terga I-II, although for this nominal taxon it is uniformly light yellow. There is a general trend for the black band between the wings to cover most of the thoracic dorsum for individuals from western China and to be reduced or absent for individuals from near the east coast. The apical terga of all of these individuals have at least some red pubescence.

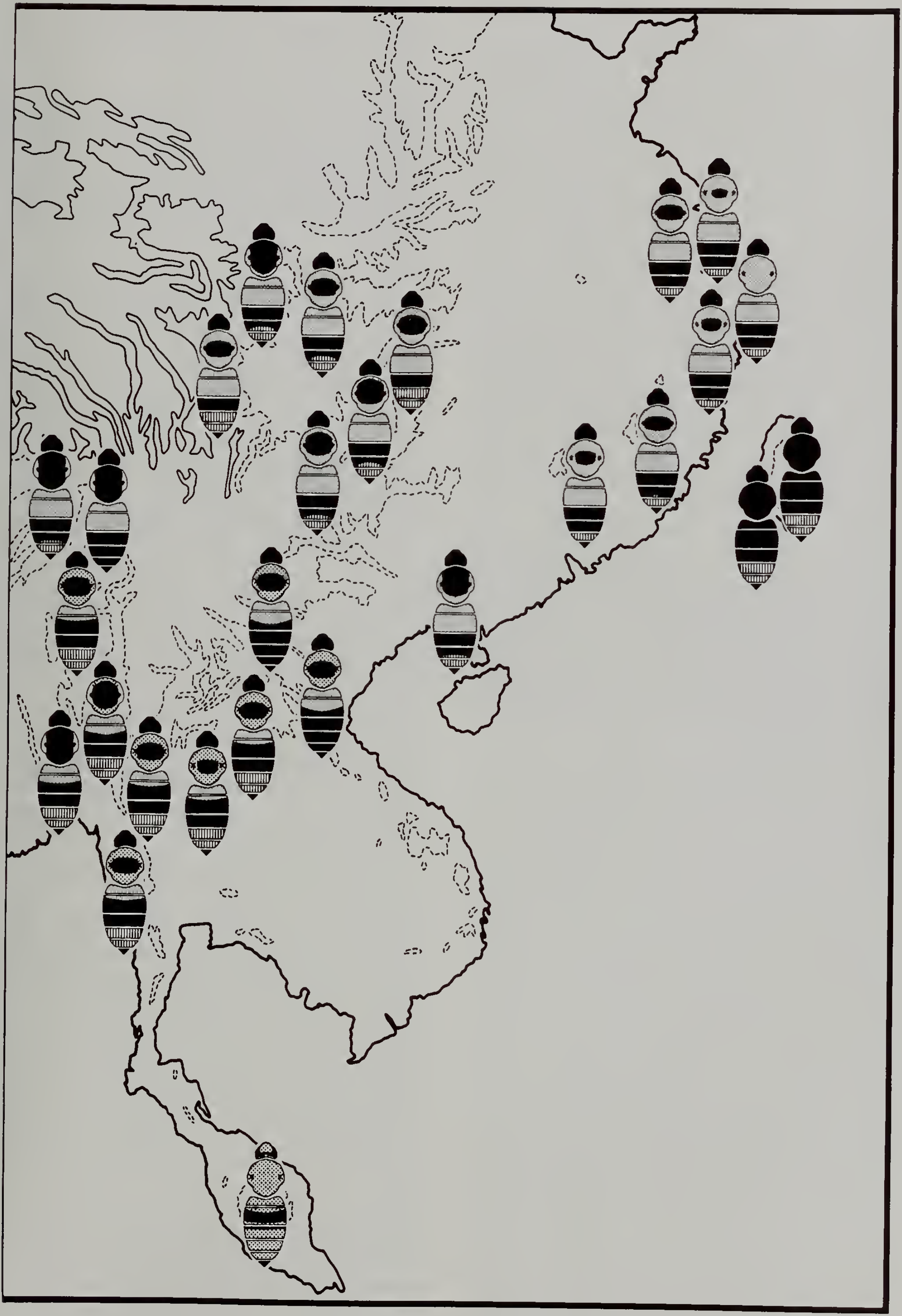
B. albopleuralis, *B. montivagus* and *B. trifasciatus* s.str. have been regarded as three separate species (e.g. Tkalců, 1968*b*, 1974*b*, 1989). No two of these three principal nominal taxa of the *trifasciatus*-group are known to occur together at any locality without intermediates, so that direct evidence for barriers to interbreeding is not available. Tkalců (1968*b*) stated that in comparison with the most similar taxon, *B. albopleuralis*, *B. montivagus* differs slightly by its longer oculomalar distance and by the stronger protrusion of its clypeus. However, individual differences between selected specimens may not be easy to interpret. For instance, the shape of the malar area at least is subject to large allometric variation with body size (Sakagami, 1972). Therefore large random samples of material from a range of localities across Asia are needed in order to examine trends in these differences in detail. Other characters of the morphology (especially of the sculpturing of the ocello-ocular areas of the females and of the sizes of the terminal process and inner hooks of the male volsellae) also vary considerably within each of these nominal taxa as well as among them, so I have been unable to find reliable morphological criteria to distinguish them. Thus in practice all three nominal taxa are still recognised by differences in the colour patterns of their pubescence.

Some individuals from intermediate areas, particularly from western China and eastern Burma, appear to show intermediate colour patterns of the pubescence between those of *B. albopleuralis*, *B. montivagus* and *B. trifasciatus* s.str. (Fig. 11). Sakagami (1972) described variation in the colour pattern of *B. trifasciatus* s.str. from western China towards that of *B. montivagus*, by replacement of the yellow hairs by black hairs at the apex of tergum II (Sakagami, 1972: fig. 6bD), and towards that of *B. albopleuralis* by replacement of the pale hairs by black hairs on the thoracic dorsum (Sakagami, 1972: fig. 6aA; a similar colour pattern was also described under the name *B. ningpoensis* subsp. *minshanicus* by Bischoff, 1936). Furthermore Richards (1931) described individuals with a colour pattern (*B. mimeticus* var. *magrettianus*, probably from central Burma, see Note 7 on the type material) that is intermediate between *B. montivagus* and *B. albopleuralis*, in that both the thoracic dorsum and most of tergum II are black-haired. I consider it likely that at least some of these intermediate colour patterns are evidence of clines between the more widespread regional colour patterns (Fig. 11). The general pattern is for individuals from the west of the range in the Himalaya to have most black hair on the thorax, to have least black hair on the gaster and to have the darkest wings, whereas individuals from the east of the range generally have the least black hair on the thorax, more on the gaster and have lighter wings. This interpretation would place all the individuals within a single interbreeding population as parts of a single species.

The names *B. wilemani* and *B. maxwelli* have been applied to populations that are isolated from other *B. trifasciatus* s.l. by sea and by tropical lowland forest respectively (Fig. 11). Both nominal taxa were originally described primarily using colour pattern characters and without comparison to any species of the subgenus *Diversobombus*. *B. wilemani* is characterised by an absence of yellow or orange-brown pubescence and by its orange-brown to nearly clear (subhyaline) wings. The tendency of individuals of *B. maxwelli* towards nearly uniformly orange pubescence converges closely with another very distantly-related species that also occurs in the Cameron Highlands of Malaysia, *B. (Pyrobombus) rufoflavus* Pendlebury (possibly conspecific with the east Himalayan *B. flavescens* Smith). The pubescence of the three workers of *B. maxwelli* in the BMNH varies from orange, with dark brown hairs intermixed on tergum II, to orange with most of terga II-III black. This dark specimen is therefore more similar in appearance to the lectotype of *B. montivagus*. Otherwise it differs by the lighter brown sclerites and slightly shallower punctures of the sculpturing of the head. I know of no evidence from which to suggest that individuals from these disjunct populations on either the island of Taiwan or in the Cameron highlands would not interbreed with those from the more widespread, northern population if they were to occur together. So *B. maxwelli* and even *B. wilemani* could be parts of a single species, *B. trifasciatus* s.l. However, I have not yet seen any males of *B. wilemani* from which to examine their characters.

DISTRIBUTION. *B. trifasciatus* is a widespread Oriental species (Map 23, Fig. 11). It is known from Taiwan (Cockerell, 1911; Skorikov, 1933*a*; Frison, 1934; Chiu, 1948; BMNH, PW, SEMK), Jiangsu (BMNH), Zhejiang (Smith, 1852*a*; Friese, 1909; Tkalců, 1960; BMNH, SEMK), Fujian (Pittioni, 1949; BMNH), Guangdong (Sakagami, 1972), Jiangxi (MNHN, PW), Hubei (Tkalců, 1960; Sakagami, 1972; PW), Gansu (Bischoff,

Fig. 11 Distribution of the colour patterns of the *trifasciatus*-group (for a colour key see Fig. 258). These individuals may all be considered to be parts of a single species, *B. trifasciatus*, depending on which species-defining criterion is accepted. The dashed line shows the 1000m contour above sea level and the solid line shows the 4000m contour. Most records are from material examined, supplemented from descriptions by Sakagami (1972: Leizhou) and by Tkalců (1968b: 5 localities in Southeast Asia).



1936; MNHU), Sichuan (Panfilov, 1957; Tkalců, 1960; Sakagami, 1972; BMNH), Yunnan (Panfilov, 1957; Tkalců, 1968*b*), Vietnam (Tkalců, 1968*b*), Laos (Tkalců, 1968*b*; BMNH), Thailand (Tkalců, 1968*b*; BMNH, PW, SEMK, ZM), Peninsular Malaysia (Pendlebury, 1923; BMNH, PW), Burma (Smith, 1878*b*; Friese, 1918; Richards, 1931; Frison, 1935; Tkalců, 1968*b*, 1989; BMNH), Manipur (BMNH), Meghalaya (Richards, 1931; Frison, 1933, 1935; BMNH), Arunachal Pradesh (BMNH), south-eastern Tibet (Wang, 1982), Sikkim (Friese, 1918; Richards, 1931; Frison, 1935; BMNH, MCSN, MNHU, UM), Darjiling Bengal (Richards, 1931; BMNH), Nepal (Richards, 1931; Tkalců, 1974*b*; BMNH, NMS, PW), Uttar Pradesh (Friese, 1916; Frison, 1935; BMNH, MNHU, PW, SEMK), Himachal Pradesh (Richards, 1931; Frison, 1933, 1935; BMNH, SEMK), Kashmir and Pakistan (Richards, 1931; Frison, 1933). A disjunct distribution between Burma and the mountains of Peninsular Malaysia is also known for *B. (Pyrobombus) flavescens* (Tkalců, 1974*b*; see the comments on *B. lemniscatus*).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. trifasciatus* is recorded from the lower slopes in the Vale of Kashmir and from the foothills of the Pir Panjal range, in the more mesic habitats in and around the lower montane coniferous forests (Map 24, Fig. 6): 6 queens, 72 workers, 9 males, from 6 localities 1000–2700 m (AB, BMNH, IZ, NR, PW, ZM, ZS).

VARIATION WITHIN KASHMIR. Almost all of the specimens from Kashmir that have been examined have the sides of the thorax black-haired and terga III-VI red. There is a small patch of yellow hairs in the middle of the basal margin of tergum III, often with a few black hairs intermixed (Figs 275–277). The only exception to this colour pattern is the holotype worker of *B. mimeticus* var. *geminatus*, labelled 'Gulmarg', which has grey-white hairs on the sides of the thorax (Fig. 278). Among the sample I collected at and around this locality during 1985 and 1986 (5 queens, 29 workers, 5 males), all specimens have the pleura entirely black-haired.

This species is closely similar in colour pattern to the local *B. haemorrhoidalis*, which occur with it at some localities outside the Vale of Kashmir (Figs 279–281, see the comments on *B. haemorrhoidalis*). It can usually be recognised by the presence of a few yellow hairs basally on tergum III, and for the females in particular, by the spinose mid basitarsus (Fig. 39) and by the broad band of punctures in the ocello-ocular area of the head. There may also be some similarity in colour pattern to some individuals of *B. biroi* (Figs 344 & 345), although the two species have not been found together. *B. biroi* has the oculo-malar distance much shorter and lacks a disto-posterior spine on the mid basitarsus.

FOOD PLANTS. (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Lupinus* sp. [introduced], unidentified pink clover-like legume; (Compositae) *Cirsium wallichii* DC.; (Acanthaceae) *Pteracanthus urticifolius* (Kuntze) Bremek.; (Labiateae) *Stachys sericea* Wallich ex Benth.

Subgenus ***ORIENTALIBOMBUS*** Richards

Orientalibombus Richards, 1929*b*: 378 (as a subgenus of *Bombus* Latreille). Type species: *Bombus orientalis* Smith, 1854: 402 = *Bombus haemorrhoidalis* Smith, by original designation.

Orientalobombus Richards; Kruseman, 1952: 102 (as a subgenus of *Bombus* Latreille). Unjustified emendation (Art. 33b(i, iii)).

For a general description of both sexes see Richards (1968).

Bombus (Orientalibombus) haemorrhoidalis Smith

(Figs 18, 40, 57, 97, 137, 177, 215, 279–281, Maps 25 & 26)

Bombus haemorrhoidalis Smith, 1852*a*: 43. Types presumed lost (see Note 1 below) [not seen].

Bombus orientalis Smith, 1854: 402. Lectotype queen by designation of Richards (1929b: 383) (see Note 2 below), INDIA: West Bengal, Darjiling (*Pearson*) (BMNH) [examined]. Change of status to *Orientalibombus haemorrhoidalis orientalis* (Smith) by Tkalců (1974*b*). **Syn. n.**

Bombus buccinatoris Smith, 1879: 132. Lectotype worker by designation of Richards (1929*b*: 384), INDIA: Himachal Pradesh, Kinnaur (BMNH) [examined]. Synonymised with *Bombus orientalis* Smith by Bingham (1897). **Syn. n.**

Bombus assamensis Bingham, 1897: 550. Lectotype male by designation of Richards (1929*b*: 384), INDIA: Assam, Margherita (*Bingham*) (BMNH) [examined]. Change of status to *Orientalibombus haemorrhoidalis* subsp. *assamensis* (Bingham) by Tkalců (1989). **Syn. n.**

Bombus (Orientalibombus) montivolans Richards, 1929*b*: 382. Holotype male by original designation [p. 383], LAOS: 'Tintoe', 1.xii.1918 (*Salvaza*) (BMNH) [examined]. **Syn. n.**

Bombus (Orientalibombus) orientalis var. *khasianus* Richards, 1929*b*: 384. Holotype worker by original designation, INDIA: Meghalaya, Khasi Hills (BMNH) [examined]. Synonymised with *Orientalibombus haemorrhoidalis pectoralis* (Friese) by Tkalců (1974*b*). **Syn. n.**

Orientalibombus montivolans subsp. *semibreviceps* Tkalců, 1968*b*: 10. Holotype worker by original designation, VIETNAM: Tonkin, Chiem Hoa, viii-ix (*Fruhstorfer*) (Zürich) [not seen]. **Syn. n.**

Orientalibombus montivolans subsp. *semicoloricontrarius* Tkalců, 1968*b*: 10. Holotype worker by original designation [p. 11], BURMA: ?Karen, 'Cheba', 900–1100 m, vi.1888 (*Fea*) (Zürich) [not seen]. **Syn. n.**

Orientalibombus haemorrhoidalis subsp. *cinnameus* Tkalců, 1989: 47. Holotype queen by original designation, BURMA: Arakan Yoma, Mount Victoria, 1400 m, iv.1938 (*Heinrich*) (MNHU) [examined]. **Syn. n.**

TYPE MATERIAL. Note 1. The abundant material from the western Himalaya agrees with the original description of *B. haemorrhoidalis*, although the type-locality is stated to be 'Chusan' [= Zhoushan, Zhejiang, eastern China]. I have not seen any specimens of the subgenus *Orientalibombus* from the region of Zhoushan. However, by analogy with the pattern of geographical variation described here for *B. trifasciatus* between Kashmir and eastern China (which closely resembles the Kashmir species of *Orientalibombus* throughout its known distribution between Kashmir and Vietnam, see the comments on *B. trifasciatus*), I would not expect any species from Zhoushan to agree in colour pattern with the original description of *B. haemorrhoidalis*. Therefore the type-locality cited is considered to be inconsistent with the description given by Smith.

Smith described *B. haemorrhoidalis* from syntypes in the Fortune collection, which was sold in 1872 without any material going to the BMNH or UM, and all syntypes are believed to be lost (D. B. Baker, pers. comm.). The Indian specimens, referred to separately by Smith in the original publication as being 'In the British Museum', cannot be considered as syntypes (Art. 72b(vi)). There is a single queen in the BMNH collection that had been acquired early enough to be one of these specimens. It bears a label 'Shang / hai', reverse side '51 / 26', and a pale blue (drawer) label 'haemorrhoidalis Smith / MSS', in handwriting identical to that of Smith. This accession number refers to 19 Hymenoptera that had been obtained in exchange with Baly for duplicates in March 1851. The area of origin is given in the accession catalogue as 'China (Shanghai)' (close to Zhoushan), but this has been crossed out and 'Northern Ind.' added in identical handwriting. Therefore this specimen is almost certainly of Indian origin and agrees with the original description and the previous interpretation of the taxon. It lacks the distal joints of all tarsi except that of the left mid leg, the apical gastral segments are curled ventrally and the pubescence has been abraded from the central area of tergum III. At some earlier stage, the gaster has also been glued back into place.

Despite the inconsistency within the original description of *B. haemorrhoidalis*, the more recent authors such as Richards (1929*b*, 1931), Frison (1933, 1935) and Tkalců (1968*b*, 1974*b*, 1989) have agreed on the identity of Smith's *B. haemorrhoidalis*. Richards (1929*b*) and Frison (1933, 1935) continued to apply *B. haemorrhoidalis* var. *albopleuralis* Friese to certain individuals of *B. (Orientalibombus) haemorrhoidalis*, although Tkalců's (1974*b*) lectotype of *B. haemorrhoidalis* var. *albopleuralis* belongs to a species of the subgenus *Diversobombus* (conspecific with *B. trifasciatus*). Nonetheless, I regard the identity of *B. haemorrhoidalis* s.str. as not in doubt, so that it is neither necessary nor valid to designate a neotype (Art. 75b).

Note 2. Two queens in the BMNH collection are candidates for having been among Smith's syntypes of *B. orientalis* in 1854. One is simply labelled 'India'. The other is labelled 'Darjeeling', reverse side 'Dr. / Pearson', with a label 'orientalis / Type Sm.', in handwriting identical to that of Smith, and with two identical accession labels '60–15 / E.I.C.'. The accessions catalogue lists this material as presented in 1860 by the Secretary of the India Board and as having included 94 Hymenoptera from Java. This might have explained the type-locality statement 'East Indies', although it has a colour pattern that is characteristic of the eastern Himalaya and the species is not known from the East Indies. However, this donation also contained 83 Hymenoptera from 'India + asiatic Islands' that is specified to have included 'Several of the Hymenoptera type specimens described by Mr Smith'. According to D. B. Baker (pers. comm.), not all of Smith's 'B.M.' syntypes were deposited in the BMNH at the time of publication. I agree with Richards (1929*b*: 383 footnote) that it is reasonable to regard the Darjiling queen as one of Smith's syntypes. Richards's use of the word 'type' in reference to this specimen is then taken to be a valid lectotype designation (Art. 74b).

AFFINITIES. The species of the subgenus *Orientalibombus* share a reduction of the interio-basal process of the male gonostylus (Fig. 177) and an extended and twisted apex of the volsella (Fig.

137) (synapomorphies). This is a morphologically divergent group with no obviously close relatives. The present interpretation is that its affinities lie with the more northern species of the subgenus *Thoracobombus* Dalla Torre rather than with those of the subgenus *Diversobombus* (in contrast to the interpretation in Williams, 1985). Species of the subgenus *Orientalibombus* share with the species of the subgenus *Thoracobombus* an apical extension of the part of the volsella beyond the pair of hooks on its inner margin (?synapomorphy). The volsella of both is also relatively broad and short, with the inner hooks placed basally on the inner apical margin, close to the inner corner.

Apart from *B. haemorrhoidalis*, the only other species of the subgenus *Orientalibombus* from the Himalaya is *B. funerarius* Smith, which is known from Sichuan (Frison, 1935; Panfilov, 1957), Yunnan (Panfilov, 1957), Burma (Skorikov, 1938*b*; Tkalců, 1989; BMNH), Darjiling Bengal and Sikkim (Friese, 1918; Richards, 1929*b*; Frison, 1935; BMNH, UM), Nepal (PW) and Uttar Pradesh (BMNH). The males of *B. funerarius* can be distinguished by their gonostyli, which are much shorter than broad in dorsal aspect, whereas those of *B. haemorrhoidalis* are nearly square, with a very much reduced interio-basal process (Fig. 177) (autapomorphy). The females of *B. funerarius* can be distinguished by the tubercles of the labrum (Richards, 1929*b*), which are unusually pronounced so that they form a transverse ridge that is only very narrowly interrupted by the median furrow. The apical impression of the clypeus is also deeper and less strongly punctured than for *B. haemorrhoidalis*.

There may be just one other species in the subgenus *Orientalibombus*, *B. braccatus* Friese (synonymised with *Bremus metcalfi* Frison by Tkalců, 1987). This is known only from Sichuan and is similar in colour pattern to the *B. trifasciatus* that also occur in Sichuan, in that the thorax and terga I-II are extensively yellow-haired (Friese, 1905). The gonostylus of the male genitalia (holotype male of *Bremus metcalfi* examined) is intermediate in outline between that of *B. funerarius* and that of *B. haemorrhoidalis* s.l. (see Frison, 1935: fig. 7c). The volsella is unique for species of this subgenus because the interio-basal hook is longer than broad and broadens slightly towards its serrated apex. I have not examined the females of *B. braccatus*.

Three principal nominal taxa have been recognised among the remaining *haemorrhoidalis*-group of the subgenus *Orientalibombus* and these were described under the names *B. montivolans*, *B. assamensis* and *B. haemorrhoidalis*. They differ from each other in colour pattern, possibly as members of regional groups of Müllerian mimics (see the discussion of the colour patterns of the Kashmir fauna). These nominal taxa are very similar in colour pattern to individuals of *B. (Diversobombus) trifasciatus*, *B. (Alpigenobombus) breviceps* Smith and *B. (Pyrobombus) rotundiceps* Friese that occur with them (see the comments on *B. trifasciatus*, *B. kashmirensis* and *B. lemniscatus* respectively; Sakagami and Yoshikawa, 1961; Tkalců, 1968*b*, 1989).

B. haemorrhoidalis is the name that has been used most recently for all of the Himalayan nominal taxa in the *haemorrhoidalis*-group (the '*haemorrhoidalis*-Gruppe' of Tkalců, 1974*b*, 1989). The pubescence of the thoracic dorsum is usually entirely black. As in the case of *B. trifasciatus*, the replacement of black by grey-white pubescence on the sides of the thorax appears to be most common among males from lower altitudes in the eastern Himalaya, at least among BMNH material. The pubescence of terga I-II is usually pale yellow. Individuals from the western Himalaya to as far east as Nepal have terga III-VI predominantly red. Individuals from eastern Nepal to as far east as Arunachal Pradesh have black pubescence on tergum III and even on tergum IV (females with more extensive black on terga III-IV and without the white pubescence on the thorax were described under the name *B. orientalis* by Smith for those with terga I-II cream-yellow, or *B. buccinatoris* for those with terga I-II more distinctly lemon-yellow; whereas similar females with yellow on terga I-II and white pubescence on the thorax were described under the name *B. orientalis* var. *khasianus* by Richards). Tkalců (1989) described a queen from Burma under the name *Orientalibombus haemorrhoidalis* subsp. *cinnameus* that has the pubescence of the thoracic dorsum black, of the sides of the thorax white, of terga I-II nearly white, of tergum III predominantly black, and of the legs orange.

The name *B. assamensis* has been applied to some specimens from Assam, which like those from northern Burma have very little or no red pubescence on the gaster. These individuals have the thoracic dorsum black, the sides of the thorax grey-white and terga I-II pale yellow.

Material from further south in the highlands of South East Asia was described under the name *B. montivolans* by Richards (1929*b*). These individuals usually have the pubescence of the thorax bright orange, though often paler at the sides, with a black band between the wing bases. The pubescence of tergum I and of the base of tergum II is pale yellow. Some specimens from above Hanoi have gastral terga III-VI black (described under the name *Orientalibombus montivolans* subsp.

semibreviceps by Tkalců, 1968*b*) as for *B. assamensis*, but individuals from most of South East Asia have red pubescence on the apical terga, as for the east Himalayan *B. orientalis*.

B. haemorrhoidalis and *B. montivolans* have been regarded as separate species (e.g. Tkalců, 1968*b*, 1974*b*, 1989). However, males of *B. haemorrhoidalis* s.str. differ only slightly from those of *B. assamensis* and *B. montivolans*, for instance in the shape of the inner hooks of the volsella (Richards, 1929*b*: figs 4–7, although another *B. assamensis* male (BMNH) has the volsella as shown in Richards's fig. 5) and of the distal margin of the gonostylus. These characters also vary within each nominal taxon. The three principal nominal taxa are not known to occur together at any locality, so that direct evidence for interbreeding is not available. Yet Tkalců (1968*b*) described an individual from central Burma under the name *Orientalibombus montivolans* subsp. *semicoloricontrarius* that could represent an intermediate between *B. orientalis* var. *khasianus* of India and *B. montivolans* of Laos. This specimen has the pubescence of both the thoracic dorsum and of tergum II almost entirely black. Furthermore, some individuals of *B. orientalis* var. *khasianus* from Assam have the red hair of terga III-VI largely replaced by black, so that they appear similar to *B. assamensis*. Therefore I consider it likely that these intermediate colour patterns are evidence of clines between the more widespread regional colour patterns. This interpretation places all of the individuals within a single interbreeding population as parts of a single species.

Distribution. *B. haemorrhoidalis* is a Himalayan and South East Asian species (Map 25). It is known from Vietnam (Tkalců, 1968*b*), Laos (Richards, 1929*b*; Tkalců, 1968*b*; BMNH), Thailand (Sakagami & Yoshikawa, 1961; Tkalců, 1968*b*; BMNH, PW, SEMK, ZM), Burma (Frison, 1933, 1935; Skorikov, 1938; Tkalců, 1968*b*, 1989; BMNH, MNHU), Yunnan (Wang, 1987), Meghalaya (Richards, 1929*b*; Frison, 1935; BMNH), Assam (Bingham, 1897; Richards, 1929*b*; BMNH), south-eastern Tibet (Wang, 1988), Arunachal Pradesh and Bhutan (BMNH), Sikkim (Friese, 1918; Richards, 1929*b*, 1930; Frison, 1935; BMNH, MCSN, PW, UM), Darjiling Bengal (Friese, 1918; Richards, 1929*b*; Frison, 1933, 1935; BMNH), Nepal (Richards, 1929*b*; Frison, 1935; Tkalců, 1974*b*; BMNH, NMS, PW), Uttar Pradesh (Richards, 1929*b*; Frison, 1935; BMNH; PW, UM, ZM), Himachal Pradesh (Smith, 1879; Richards, 1929*b*; Frison, 1933, 1935; BMNH), Kashmir and Pakistan (Richards, 1929*b*; Frison, 1933). There is also a dubious record from the Indian plains at Calcutta (Dover, 1922).

Material examined from Kashmir. In Kashmir, *B. haemorrhoidalis* is recorded from the foothills of the Pir Panjal range (at Patnitop it was found in humid gullies in the coniferous forest) (Map 26): 8 queens, 102 workers, 1 male, from 3 localities 1000–2000 m (BMNH, NR, PW).

Variation within Kashmir. All of the females from Kashmir have the sides of the thorax black-haired and terga III-VI red, with only a few black hairs intermixed in the middle of tergum III, near the base (Figs 279–281). Only the male has grey-white hairs intermixed on the lower sides of the thorax (Fig. 281).

This species is closely similar in colour pattern to the *B. trifasciatus* that occur with it (Figs 275–277). It can usually be recognised by the absence of any yellow hairs at the base of tergum III, and for the females in particular, by the absence of the spine on the mid basitarsus (Fig. 40), and by the broad area without punctures on the ocello-ocular area of the head (Fig. 215). At the lower altitude of Muzaffarabad (1000 m, 15.x.1953), *B. haemorrhoidalis* was apparently far more abundant (93/94 workers) than *B. trifasciatus* (1/94 workers). Higher up, at Patnitop (2000 m, 6–8.ix.1986), *B. haemorrhoidalis* was less abundant (8/31 workers) than *B. trifasciatus* (23/31 workers).

Food plants. (Balsaminaceae) *Impatiens glandulifera* Royle; (Acanthaceae) *Pteracanthus urticifolius* (Kuntze) Bremek.

Subgenus ***SUBTERRANEOBOMBUS*** Vogt

Subterraneobombus Vogt, 1911: 62 (as a subgenus of *Bombus* Latreille). Type species: *Apis subterranea* Linnaeus, 1758: 579 = *Bombus subterraneus* (Linnaeus), by subsequent designation of Frison (1927: 68).

Subterraneibombus Vogt; Skorikov, 1938*a*: 145. Unjustified emendation (Art. 33b(i, iii)).

For a general description of both sexes see Richards (1968).

Bombus (Subterraneobombus) melanurus Lepeletier

(Figs 58, 59, 98, 99, 138, 139, 178, 179, 282–290, Maps 27 & 28)

Bombus melanurus Lepeletier, 1836: 469. Lectotype queen by designation of Tkalců (1969*a*: 202), SYRIA: no further data (UM) [examined].

Bombus Tschitscherini Radoszkowski, 1862: 591 [by indication of Radoszkowski, 1859: 485]. Holotype queen by monotypy (see Note 1 below), U.S.S.R.: 'Transoural', no further data (ZI) [not seen]. Recombined as *Bombus melanurus tschitscherini* Radoszkowski by Vogt (1909). **Syn. n.**

Bombus difficillimus Skorikov, 1912*b*: 609. Lectotype queen by designation of Podbolotskaya (in press), U.S.S.R.: Tadzhikistan S.S.R., Pamir, 3700 m, 15.vi.1909 (*Makarjin*) (ZI) [examined]. Change of status to *Bombus melanurus difficillimus* Skorikov by Reinig (1934). Provisional synonym.

Bombus (Subterraneobombus) melanurus subsp. *subdistinctus* Richards, 1928*b*: 333. Holotype queen by original designation, INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (BMNH) [examined]. **Syn. n.**

Bombus (Subterraneobombus) melanurus subsp. *griseofasciatus* Reinig, 1930: 83. 36 syntype queens, 38 syntype workers, 16 syntype males, U.S.S.R.: Tadzhikistan S.S.R., Pamir, 3700–4500 m, 5.vii- 29.viii.1928 (ITZ) [not seen]. Synonymised with *Bombus melanurus difficillimus* Skorikov by Reinig (1934). Provisional synonym.

Bombus (Subterraneobombus) maidli Pittioni, 1939*b*: 246. LECTOTYPE worker by present designation (see Note 2 below), MONGOLIA: north, no further data, 1892 (*Leder*) (NM) [examined]. Synonymised with *Megabombus subdistinctus* (Richards) by Tkalců (1969*a*). **Syn. n.**

TYPE MATERIAL. Note 1. Radoszkowski described *B. tschitscherini* from a single queen sent to him by E. Eversmann that had a band of black pubescence between the wings. If just a single specimen can be found in the ZI collection that bears labels with the appropriate data, this would be regarded as the holotype (Art. 73a(ii)).

Note 2. Pittioni described *B. maidli* from one queen, one male and three workers. There is a single worker in the NM collection with (1) a red printed label 'Type'; (2) a printed label 'N. Mongolei / Leder 92'; (3) '*melanurus* / det. Kohl.'; (4) '*Subterraneob. / maidli* Pitt. [worker] / det. Pittioni' in handwriting identical to that of Pittioni; (5) 'B. MAIDLI / MAIDLI PITT. / DET. PITTIONI, 1936'; (6) 'LECTOTYPE / B. (S.) / maidli Pitt. / Tkalců det.' [designation not published]; (7) a red printed label 'Lecto- / typus'. This specimen, which lacks the right mid basitarsus, is designated as lectotype (Art. 74a).

AFFINITIES. A strongly inwardly-curved apex of the penis valve head is shared by a large group of bumble bees, which in Kashmir includes the species of the subgenera *Subterraneobombus, Alpigenobombus, Pyrobombus*, *Sibiricobombus* and *Melanobombus* (Figs 58–71, 76–85) (synapomorphy, secondarily much modified for *Bombus* s.str., Figs 72–75). The species of the subgenus *Subterraneobombus* share a particularly pronounced broadening of the penis valves in lateral aspect, in which the ventro-basal angle is produced and broadened across the penis valve axis, into a toothed paddle-like form (Figs 98–100) (synapomorphy). The male gonostylus has the interio-basal process broadened antero-posteriorly (synapomorphy) and, for most species (?secondarily reduced for *B. fedtschenkoi* Morawitz), curved ventrally (Figs 178–180).

The male genitalia of *B. melanurus* may be unique for males of the subgenus *Subterraneobombus*, in that the head of the penis valve lacks a strong posteriorly-directed process from the dorsal exterior part of its base (Figs 58 & 59) and the interio-basal process of the gonostylus does not become broader distally (Figs 178 & 179) (plesiomorphies within the subgenus *Subterraneobombus*) (see Reinig, 1930: fig. 5). This distinguishes *B. melanurus* from *B. fragrans* Pallas, which also occurs in the central Asian steppes, but with a more western and northern distribution (distribution maps for both are provided by Skorikov, 1931: figs 5, 9; see also Panfilov, 1984: map 192). The head of the penis valve is not shortened and broadened for either of these species as it is for *B. fedtschenkoi* Morawitz, *B. personatus* (Fig. 60) and the species of the *subterraneus*-group (synapomorphy of *B. fedtschenkoi* + *B. personatus* + *subterraneus*-group, see the comments on *B. personatus*). Neither is the head of the penis valve strongly directed ventrally as it is for species of the *subterraneus*-group alone (synapomorphy of the *subterraneus*-group).

The females of *B. melanurus* can be distinguished from *B. fragrans*, *B. amurensis* Radoszkowski from Siberia and from *B. fedtschenkoi* (which is closely similar in colour pattern) from the Tien Shan ranges, by its virtually unpunctured central area of the clypeus (Skorikov, 1914*b*). The oculo-malar distance is much longer than the breadth of the mandible at its base for *B. melanurus*, but scarcely longer than this breadth for *B. fragrans* or *B. amurensis*. I have seen no males of *B. amurensis*. *B. flaviventris* is another species that has been placed in the subgenus *Subterraneobombus* together with these species with a relatively short oculo-malar distance (Richards, 1930), although the material in the BMNH collection shows many character states in common with species of the subgenus *Sibiricobombus* (see the comments on *B. oberti*).

B. melanurus s.str. was originally described from a queen with a yellow thoracic dorsum that lacks a band of black hair between the wing bases. Individuals with this colour pattern, which also have the wings clouded with brown (infuscated), occur in Turkey, the Tien Shan ranges and Kashmir. The pale pubescence varies from brown to lemon-yellow in colour (e.g. Figs 283 & 288). Richards (1928*b*) described the individuals from Kashmir with this unbanded colour pattern, but with wings that 'are, on the average, much less dark than usual' (see Tkalců, 1969*a*: plate facing page 200), under the name *B. melanurus* var. *subdistinctus*. Tkalců (1969*a*) concluded that this is a separate species, noting the presence of a small posteriorly-directed tooth on the posterior part of the penis valve head as another distinguishing character. However this tooth is not present for all individuals (Figs 58 & 59), or even for both penis valves of some individuals. Pittioni (1939*b*) also described some unbanded individuals from Mongolia that have the yellow pubescence particularly extensive on the sides of the thorax under the name *B. maidli*. All of these individuals from Kashmir and Mongolia are otherwise closely similar to other *B. melanurus*, so there is no reason to believe that they are not all parts of the same species.

Individuals of the '*melanurus*-Gruppe' (Tkalců, 1974*a*, 1974*b*) from further east in Mongolia and Gansu (e.g. Skorikov, 1931: fig. 9) usually have a band of black hair between the wing bases. The name *B. tschitscherini* was applied to these banded individuals by Radoszkowski (1859, 1862). The pale pubescence and the wings are similar in shade to the darker individuals of *B. melanurus* s.str. The male genitalia (Reinig, 1930: fig. 5; Tkalců, 1974*a*: figs 28–32) are very similar to those of *B. melanurus* s.str., but the females have a broader band of punctures in the oculo-ocellar area, there are more micropunctures in the middle of the clypeus, and the pubescence is particularly short and even.

Some of the individuals from Mongolia and from further south in the Tibetan massif and the higher Pamir ranges resemble *B. tschitscherini* in that they have a black band between the wings, although the pale pubescence is lemon-yellow or cream and the wings are nearly clear (subhyaline). These individuals were first described under the name *B. difficillimus* by Skorikov (resembling Fig. 282). Reinig apparently redescribed this taxon under the name *B. melanurus* subsp. *griseofasciatus*, because he subsequently synonymised the two (Reinig, 1934). I have not seen any males, but the male genitalia (Reinig, 1930: fig. 5, under the name '*B. mel. griseofasciatus*') appear to be very similar to those of *B. melanurus* s.str. The females have the band of punctures in the ocello-ocular area intermediate in breadth between the other two nominal taxa. However, the inner corners of the labral tubercles are usually more narrowly acute so that the sides of the longitudinal median furrow converge throughout its length, the micropunctures are completely absent from the middle of the clypeus, the disto-posterior angle of the mid basitarsus is less strongly produced, and the pubescence is particularly long and uneven.

There is considerable and possibly continuous variation among individuals within each of these nominal taxa in the colour pattern, in the shade of the pale pubescence and of the wings, and in the morphological characters. Therefore there is no good evidence as yet from which to suggest that these nominal taxa are not just divergent parts of a single interbreeding population and so parts of a single species. *B. melanurus* and *B. difficillimus* have not been found together in the Pamir ranges (Reinig, 1930: fig. 2) or in Kashmir. However, they do occur at low density on opposite sides of at least one of the ridges of the Zanskar mountains (at Chogdo & Nimaling), where *B. difficillimus* occupies the higher valley. Of course more information is needed concerning interbreeding between them in order to establish their status more definitely.

Nests from the Pamir were described by Reinig (1930) and by Bischoff (1931).

DISTRIBUTION. *B. melanurus* is a widespread, but primarily central Asian species (Map 27). It is known from Mongolia (Pittioni, 1939*b*; Skorikov, 1933*a*; Bischoff, 1936; Tkalců, 1974*a*; BMNH, NM, PW), the Altai (BMNH), the Tien Shan (Skorikov, 1931; Bischoff, 1936; Panfilov, 1957; BMNH), the Pamir (Skorikov, 1912*b*, 1931; Reinig, 1930, 1934; Bischoff, 1931; ZI), the Hindu Kush (Reinig, 1940; Richards, 1951; Tkalců, 1969*a*; BMNH), Pakistan (Frison, 1935; BMNH, PW), Kashmir, Xinjiang [Kunlun Shan] (Morawitz, 1886), Himachal Pradesh (PW), Uttar Pradesh (BMNH), Nepal (Tkalců, 1974*b*; BMNH, NMS), Sikkim (Richards, 1928*b*, 1930; BMNH), Tibet (Richards, 1928*b*, 1930; Wang, 1982; BMNH), Qinghai (Morawitz, 1886; Skorikov, 1912*b*; Panfilov, 1957; Tkalců, 1961; Wang, 1982; ZS), Gansu (Bischoff, 1936; MNHU), Inner Mongolia (Skorikov, 1933*a*) and Shanxi (Yasumatsu, 1951). In the west it is also known from western Iran (BMNH), the Caucasus (Skorikov, 1931), Turkey (Skorikov, 1931; Reinig, 1971; BMNH), Syria (UM) and Lebanon (BMNH). Part of this distribution is mapped by Skorikov (1931: fig. 9). A similar disjunct distribution between the Hindu Kush ranges on the one hand and the Elburz and Armenian highlands on the other is shown by *B. keriensis*.

MATERIAL EXAMINED FROM KASHMIR. *B. melanurus* is widespread in Kashmir, recorded from the Hindu Raj, Karakoram, Ladakh, Zanskar, Great Himalaya and Pir Panjal ranges, in montane coniferous forest, alpine scrub and steppe and in high, subtropical semi-desert (Map 28, Fig. 6): 85 queens, 186 workers, 135 males, from 29 localities 1800–4800 m (AB, BMNH, FA, MI, NR, PW, RH, ZM).

VARIATION WITHIN KASHMIR. Queens and workers are often poorly differentiated in size. Although the colour pattern of this species is apparently stable over large areas of its distribution, there is considerable variation within Kashmir. Queens from the upper forest on Mt Apharwat (2700–3400 m, 9/9 queens) have the pale pubescence brown rather than yellow (Fig. 288). These queens are all likely to be old, over-wintered individuals because they have very torn wing margins. Young queens seen at Gulmarg, all of the queens from Leh (3500 m, 5/5 queens, Fig. 283), and workers generally (Figs 284, 287, 289), have the pale pubescence slightly paler and more sand-yellow to lemon-yellow.

Queens from Nimaling (4800 m, 3/3 queens) have the pale pubescence lemon-yellow to almost cream. These queens, and another from Burzil Chauki, also have well-defined and broad bands of black hairs between the wing bases (Fig. 282, the pattern described under the name *B. difficillimus*, Map 28). The presence of a few black hairs on the thoracic dorsum, especially just above the wing bases, is common among workers from Gulmarg. The black hairs sometimes form a diffuse band between the wings, which is particularly obvious for a few, fresh workers from Gulmarg (3/26 workers, Fig. 287), and for a queen from Chittakatha Sar (4600 m, Fig. 286), above the Kishanganga valley. There is also some variation in the extent of the yellow pubescence on the sides of the thorax. This yellow pubescence usually occupies the dorsal half of the area between the wing bases and the leg bases, but may occupy nearly all of this area for some workers and even extends onto the legs in males.

This species is distinctive in its appearance at most localities. At high altitudes, workers with a black band between the wing bases (cf. Fig. 282) may resemble *B. personatus* (Fig. 292, see the comments on *B. personatus*). At a few localities in the Great Himalaya range, it may be closely similar in colour pattern to some individuals of *B. asiaticus* that lack red pubescence on the apical terga (e.g. Fig. 278), but it is recognisable by the shiny outer surface of the hind tibia and by the lack of dense, short hair at the base of the hind basitarsus (see the key, couplet 11).

FOOD PLANTS. **Kashmir**: (Ranunculaceae) *Aconitum hookeri* Stapf; (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC.; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Verbascum thapsus* L., *Digitalis lanata* Ehrh. [introduced], *D. purpurea* L. [introduced]; (Labiateae) *Stachys sericea* Wallich ex Benth., *Thymus linearis* Benth. ex Benth.; (Polygonaceae) *Bistorta viviparia* (L.) Gray.

Ladakh: (Leguminosae) *Medicago falcata* L., *Caragana versicolor* (Wallich) Benth.; (Compositae) *Echinops cornigerus* DC.; (Scrophulariaceae) *Verbascum thapsus* L.; (Labiateae) *Stachys tibetica* Vatke, *Nepeta podostachys* Benth.

Bombus (Subterraneobombus) personatus Smith

(Figs 60, 100, 140, 180, 291–294, Maps 29 & 30)

Bombus personatus Smith, 1879: 132. Lectotype queen by designation [Art. 74b] of Richards (1930: 656), INDIA: Himachal Pradesh, Kinnaur (BMNH) [examined].

Bombus Roborowskyi Morawitz, 1886: 197. Lectotype queen by designation of Podbolotskaya (in press), CHINA: Qinghai, Burhan Budai Shan, 14000 ft [4300 m] (*Prshewalski*) (ZI) [examined]. **Syn. n.**

AFFINITIES. Within the subgenus *Subterraneobombus* (see the comments on *B. melanurus*), *B. personatus* belongs to a group of species for which the penis valve head is shortened and broadened (Fig. 60) and the interio-basal process of the gonostylus becomes broader distally (Fig. 180) (synapomorphies of *B. fedtschenkoi* + *B. personatus* + *subterraneus*-group; this entire group is the broader, more inclusive '*subterraneus*-Gruppe' described from other characters by Tkalců, 1974*a*). However, for *B. personatus* and *B. fedtschenkoi* the penis valve head is not as strongly directed ventrally as for members of the *subterraneus*-group (Fig. 100) (synapomorphy of the *subterraneus*-group).

B. fedtschenkoi is known from the Tien Shan region (Skorikov, 1914*b*; Skorikov, 1931; BMNH). *B. fedtschenkoi* lacks an apically directed interio-basal process of the male gonostylus (autapomorphy; see Reinig, 1930: fig. 5; Skorikov, 1931:

fig. 35). *B. personatus*, like *B. melanurus*, has no large punctures in the middle of the clypeus, but there are more micropunctures. These punctures are not nearly as large as those of *B. fragrans, B. amurensis,* or *B. fedtschenkoi*. The oculo-malar distance of females of *B. personatus* is relatively longer than that of even the larger *B. melanurus* (see the comments on *B. melanurus*) and has fewer punctures.

Morawitz described queens from Qinghai under the name *B. roborowskyi*. The lectotype is closely similar to the lectotype of *B. personatus* and is believed to be part of the same species. It is possible that *B. personatus* may even be conspecific with *B. difficillimus* var. *pamirus* Skorikov from the Pamir ranges (Skorikov, 1912*b*, 1931), although the oculo-malar distance is apparently shorter for this nominal taxon (for a discussion of the identity of this nominal taxon, see also Reinig, 1930, 1934; and the comments on *B. oberti*). I have seen no material of *B. difficillimus* var. *pamirus*.

DISTRIBUTION. *B. personatus* is a Tibetan species (Map 29). It is known from Kashmir, Himachal Pradesh (Smith, 1879; BMNH), Tibet (Richards, 1930; Wang, 1982; BMNH), Qinghai (Morawitz, 1886; Panfilov, 1957; Tkalců, 1961; Wang, 1982; ZI, ZS) and Gansu (Morawitz, 1890).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. personatus* is recorded from the Zanskar ranges, in the high, dry alpine steppe (Map 30): 12 queens, 2 workers, 2 males, from 2 localities 3500–4800 m (BMNH, FA, PW).

I found what could have been the site of a nest on Nimaling plain (4800 m, 23.ix.1986). A queen was seen to fly from, and later to return to, a hole at the base of a dry-stone wall in a shepherd's summer hut.

VARIATION WITHIN KASHMIR. The pale pubescence of the thorax and of terga I-II varies from lemon-yellow (only on terga I-II) to pale sand-yellow to almost cream. For queens and males, the pubescence of terga III-V has many cream-white hairs along the posterior margin (Figs 291, 293, 294), but pale hairs may be very few in this position in workers (Fig. 292).

This species is usually distinctive in its appearance, although workers (Fig. 292) may resemble the individuals of *B. melanurus* with a black band between the wing bases, which are known to occur with them (cf. Fig. 282). These dark workers of *B. personatus* can be recognised by their pale hairs on the leg bases and on the sterna.

FOOD PLANTS. (Leguminosae) *Caragana versicolor* (Wallich) Benth.; (Labiateae) *Stachys tibetica* Vatke.

Subgenus ***ALPIGENOBOMBUS*** Skorikov

Alpigenobombus Skorikov, 1914*a*: 128. Type species: *Alpigenobombus pulcherrimus* Skorikov, 1914*a*: 128 = *Bombus kashmirensis* Friese, by present designation.

Mastrucatobombus Krüger, 1917: 66 (as a subgenus of *Bombus* Latreille). Type species: *Bombus mastrucatus* Gerstaecker, 1869: 326 = *Bombus wurflenii* Radoszkowski, by monotypy. Synonymised with *Alpigenobombus* Skorikov by Richards (1928*b*).

Alpigenobombus Skorikov; Frison, 1927: 64 (as a subgenus of *Bombus* Latreille).

[*Nobilibombus* Skorikov, 1933*a*: 62. Published without fixation of type species, unavailable name (Art. 13b).]

[*Nobilibombus* Bischoff, 1936: 12 (as a subgenus of *Bombus* Latreille). Type species: *Nobilibombus morawitziides* Skorikov, 1933*a*: 62 = *Bombus nobilis* Friese, by monotypy. Published as a junior synonym of *Alpigenobombus* Skorikov, unavailable name (Art. 11e).]

Alpigenibombus Skorikov; Skorikov, 1938*b*: 1. Unjustified emendation (Art. 33b(i, iii)).

[*Nobilibombus* Milliron, 1961: 54 (as a subgenus of *Pyrobombus* Dalla Torre). Type species: *Bombus nobilis* Friese, 1905: 513 [cited as *Bombus nobilis* Skorikov], by original designation. Published as a junior synonym of *Pyrobombus* Dalla Torre, unavailable name (Art. 11e).]

Nobilibombus Richards, 1968: 222 (as a subgenus of *Bombus* Latreille) (see Note 2 below). Type species: *Bombus nobilis* Friese, 1905: 513, by original designation. Syn. **n.**

Note 1. Skorikov (1914*a*) originally included '*B. lefebvrei* Lep. (= *B. mastrucatus* auct.)' and *A. pulcherrimus* Skorikov in his genus *Alpigenobombus*. Unfortunately he did not clearly and unambiguously designate a type species (Art. 67c) and *B. alpigenus* cannot be the type species of *Alpigenobombus* by absolute tautonomy. Frison's (1927: 64) subsequent designation of *Bombus alpigenus* Morawitz as type species is invalid because this species was not specifically included by Skorikov in the original publication (Art. 67g). Skorikov's original reference to *B. lefebvrei* Lepeletier is a misidentification, because Lepeletier's holotype belongs to a species (oldest available name *B. pomorum* (Panzer)) of the distantly related subgenus *Rhodobombus* Dalla Torre (Løken, 1973), whereas Skorikov cites *B. mastrucatus* auct. (conspecific with *B. mastrucatus* Gerstaecker, for which the oldest available name is *B. wurflenii* Radoszkowski) as a synonym.

Designation of Skorikov's *Alpigenobombus lefebvrei* as the type species would require the ICZN to decide the identity of this nominal taxon (Art. 70b). Therefore I designate *Alpigenobombus pulcherrimus* Skorikov as the type species of *Alpigenobombus* Skorikov because its identity is clear and this fixation maintains the stability of usage of *Alpigenobombus* Skorikov.

Note 2. Skorikov (1933*a*) originally included *Nobilibombus nobilis* (Friese), *Nobilibombus validus* (Friese) and *Nobilibombus morawitziides* Skorikov in his genus *Nobilibombus*, but did not designate a type species. Richards (1968) considered *B. nobilis* Friese to be the type species of *Nobilibombus* Skorikov by virtual tautonymy, although this is not sufficient under the present code, which requires absolute tautonymy (Art. 68e). However, Richards's reference to *B. nobilis* Friese as the type species is sufficient as an original designation for the subgenus *Nobilibombus* Richards (Art. 68b). Unfortunately no putative syntype of *B. nobilis* has yet been found that agrees with the original description in having four or five teeth on the mandibles (see the comments on *B. pyrosoma*; Richards, 1968: 222). Nonetheless the identity of *B. nobilis* is not in doubt, so the designation of a neotype is neither necessary nor valid (Art. 75b).

For a general description of both sexes see the descriptions of the subgenera *Alpigenobombus* and *Nobilibombus* by Richards (1968). These two groups were originally distinguished primarily on the basis of the greater oculo-malar distance for the individuals ascribed to *Nobilibombus*. I agree with Bischoff (1936) that placing all the species together in a single group, by considering *Nobilibombus* Richards as a junior subjective synonym of *Alpigenobombus* Skorikov, emphasises their many similarities (e.g. Ito, 1985; Williams, 1985).

Bombus (Alpigenobombus) kashmirensis Friese

(Figs 25, 29, 33, 37, 61–63, 101–103, 141–143, 181–183, 295–310, Maps 31 & 32)

Bombus mastrucatus var. *kashmirensis* Friese, 1909 [September, see Tkalců, 1974*b*]: 673 [redescribed by Friese & Wagner, 1910: 47]. Lectotype queen by designation of Tkalců (1974*b*: 327), INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (MNHU) [examined].

Bombus mastrucatus var. *stramineus* Friese, 1909: 673 [redescribed by Friese & Wagner, 1910: 47]. Type worker presumed lost (Tkalců, 1974*b*: 327), INDIA: Kashmir, no further data [not seen]. Synonymised with *Alpigenobombus kashmirensis* (Friese) by Tkalců (1974*b*) (see Note 1 below).

Bombus tetrachromus Cockerell, 1909 [November, see Tkalců, 1974*b*]: 397. Holotype queen by original designation, PAKISTAN: Baltistan (BMNH) [examined]. Synonymised with *Alpigenobombus kashmirensis* (Friese) by Tkalců (1974*b*).

Alpigenobombus pulcherrimus Skorikov, 1914*a*: 128. Holotype queen by monotypy (see Note 3 below), INDIA: Kashmir, Zoji La, above 3000 m, 12–15.vi.1912 (*Jacobson*) (ZI) [not seen]. Synonymised with *Bombus tetrachromus* Cockerell by Richards (1930).

[*Alpigenobombus (Alpigenobombus) beresovskii* Skorikov, 1922: 156. Published without description or indication, unavailable name (Art. 12a).]

Alpigenobombus (Alpigenobombus) kashmirensis (Friese); Skorikov, 1922: 156

Bombus (Mastrucatobombus) mastrucatus subsp. *meinertzhageni* Richards, 1928*b*: 335. Holotype queen by monotypy (see Note 4 below), INDIA: Kashmir, Ladakh, Chushul, 1925 (*Meinertzhagen*) (BMNH) [examined]. Synonymised with *Alpigenobombus kashmirensis* (Friese) by Tkalců (1974*b*).

[*Bombus (Alpigenobombus) tetrachromus* var. *albohirtus* Richards, 1930: 637 [examined]. Infrasubspecific (see Note 2 below) (Art. 45g(ii)(1)), unavailable name (Art. 45e).]

[[*Alpigenobombus*] *beresovskii* Skorikov, 1931: 204. Published without description, unavailable name (Art. 13a).]

Alpigenobombus beresovskii Skorikov, 1933*b*: 248. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, CHINA: Sichuan, 'Yach Zhou', 28.iii–5.iv. 1893 (*Potanin*) (ZI) [examined]. **Syn. n.**

NOMENCLATURE. Note 1. Following the Principle of the First Reviser (Art. 24), *B. kashmirensis* is accepted in precedence to *B. stramineus* by the action of Skorikov (1922).

Note 2. Richards's use (1930: 634 etc.) of the term 'Subsp.' elsewhere in his paper is taken to indicate that infrasubspecific rank is meant for *B. tetrachromus* var. *albohirtus*. No subsequent author has either adopted the name *albohirtus* for a taxon in the species group or regarded it as a senior homonym, so Richards's taxon is deemed to be of infrasubspecific status (Art. 45g(ii)(1)).

TYPE MATERIAL. Note 3. Skorikov's description of *Alpigenobombus pulcherrimus* s.str. specifies that only a single queen was available. If a single queen with the appropriate data can be found then this should be regarded as the holotype (Art. 73a(ii)).

Note 4. Richards described *B. mastrucatus meinertzhageni* from 'One female from Shusal' [= Chushul]. A single queen in the BMNH collection agrees with the original description and carries the data quoted. It also bears a label 'B. tetrachromus / var. *meinertz- / -hageni*, / Type. Richards', in handwriting identical to that of Richards. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. A dorso-ventrally flattened and sickle-shaped head of the penis valve is shared by a large group of bumble bees, which in Kashmir includes the species of the subgenera *Alpigenobombus, Pyrobombus, Sibiricobombus*, and *Melanobombus* (Figs 61–71, 76–85) (synapomorphy, secondarily much modified for *Bombus* s.str., Figs 72–75). Females of species of the subgenus *Alpigenobombus* share the development of six teeth on the distal margin of the mandible (Fig. 33, ?synapomorphy).

Within the subgenus *Alpigenobombus*, females of the *breviceps*-group share a particularly pronounced development of the two pre-apical teeth of the mandible, which are acute, and the adjacent incisura is deeper than its own width (?synapomorphy of the *breviceps*-group). This group includes *B. grahami* (Frison), *B. genalis* Friese and *B. breviceps*. The males of the Chinese and east Himalayan (Richards, 1930; Frison, 1935; Skorikov, 1938*b*; Wang, 1987, 1988; BMNH, IZ, PW) *B. genalis* are not known. The males of *B. breviceps* have the gonostylus reduced apically to a transverse band, although this retains a strongly produced, interio-basal process and a strongly produced interio-apical corner (see Frison, 1935: fig. 5). The recurved hook of the penis valve head is short, as for *B. nobilis*, but more broadened. The males of the Chinese and east Himalayan (Frison, 1933, 1935; Wang, 1982; BMNH) *B. grahami*, which I have not seen, are apparently intermediate in these character states between *B. nobilis* and *B. breviceps* (Frison, 1935: fig. 6).

The Chinese *B. breviceps* Smith is very similar in morphology to the west Chinese and Himalayan *B. dentatus* Handlirsch, which has the orange pubescence of the thoracic dorsum replaced by black. Individuals with intermediate colour patterns have been described (see Tkalců, 1968*b*). Therefore these nominal taxa are likely to be parts of a single species that is widespread from China throughout much of South East Asia and the Himalaya (records in e.g. Smith, 1852*a*; Frison, 1935; Bischoff, 1936; Skorikov, 1938*b*; Tkalců, 1960, 1968*b*; Sakagami, 1972; Wang, 1987; BMNH, MCSN, MNHN, PW, SEMK, UM). This species, which resembles *B. trifasciatus* and *B. haemorrhoidalis* in colour pattern (see the comments on these species and Fig. 11), may also be present in the foothills of south-eastern Kashmir (oldest available name for *B. orichalceus* Friese, unconfirmed record from Kashmir by Skorikov, 1933*b*; there is also a queen in the BMNH from Dalhousie, just across the border from Kashmir in Himachal Pradesh).

The females of *B. wurflenii, B. kashmirensis* and *B. nobilis* have the incisura wider than deep and the two pre-apical teeth of the mandible are weak and obtuse (Fig. 33, ?plesiomorphic among species of the subgenus *Alpigenobombus*). Males of these species have the interio-apical process of the volsella reduced (Figs 141–143) (?plesiomorphic among species of the subgenus *Alpigenobombus*). The males of *B. nobilis* can be distinguished from those of *B. kashmirensis* by their shorter gonostylus, which has the apical margin concave rather than straight or convex (Figs 181–183), and by the shorter recurved hook of the penis valve head (these character states appear to be intermediate between *B. kashmirensis* and *B. breviceps*). The females of *B. nobilis* have the oculo-malar distance just greater than the breadth of the mandible at its base, rather than distinctly shorter than this breadth as for *B. kashmirensis* and *B. wurflenii*. I have seen material of the banded yellow *B. nobilis* Friese from Sichuan (BMNH, PW), Yunnan, northern Burma, south-eastern Tibet and Sikkim (BMNH, UM), Nepal (PW) and Uttar Pradesh (BMNH). *B. validus* Friese (synonymised with *Nobilibombus morawitziides* Skorikov by Tkalců, 1987), which has the pale pubescence of the thorax grey-white rather than yellow, is otherwise closely similar to *B. nobilis* and may be part of the same species. I have seen material of this nominal taxon from Gansu (ZI), northern Burma, south-eastern Tibet and Sikkim (BMNH) and Nepal (PW). Females of two further nominal taxa from Qinghai, Tibet and Yunnan (*B. xizangensis* and *B. chayaensis*), both very similar to *B. nobilis*, have been described by Wang (1979, 1982, 1987, 1988) from slight differences in the colour pattern (not seen).

Apart from species of the *breviceps*-group and *B. nobilis*, the subgenus *Alpigenobombus* may otherwise include just two species that show great variation in the colour patterns of the pubescence. *B. wurflenii* Radoszkowski [the correct original spelling of *B. wurfleini* of authors] is a European species that reaches eastwards as far as the Caucasus and the Urals (e.g. Reinig & Rasmont, 1988: fig. 1; BMNH). The females of *B. wurflenii* are closely similar to those of *B. kashmirensis* in morphology. The clypeus of *B. wurflenii* has widely-spaced, moderate or small punctures throughout, whereas for *B. kashmirensis* the punctures are slightly more widely-spaced in the middle of the clypeus, so that there is an almost unpunctured, shining area. However, the males can be separated more easily because, from the anterior aspect, the eyes of *B. wurflenii* (not noticeably enlarged relative to the female) are at their broadest in their ventral half, whereas the (enlarged) eyes of *B. kashmirensis* are broadest in their dorsal half. The genitalia of males of *B. kashmirensis* and of *B. wurflenii* are closely similar, but the recurved hook of the penis valve head is more narrowed to a point for *B. wurflenii* and the apex of the gonocoxite is narrower.

Differences in eye size between males of *B. kashmirensis* and *B. wurflenii* are associated with differences in mate-searching behaviour (see the introduction on male mate-searching behaviour). *B. wurflenii* is widespread in Europe among the upper montane forests, where males patrol circuits of scent-marked sites within the forests to find mates (pers. obs.). *B. kashmirensis* is widespread in the Himalaya and Tibet among the high alpine zones. On Mt Apharwat in Kashmir, the males hover near the peak and watch for potential mates. Individuals from these populations of *B. wurflenii* and *B. kashmirensis* would be unlikely to interbreed even if they were to occur on the same mountain, because they appear to search for mates in different ways and in different kinds of habitat (cf. comments on *B. rufofasciatus*, *B. asiaticus* and *B. hypnorum*).

The queen from Ladakh described by Richards (1928*b*) under the name *B. mastrucatus* subsp. *meinertzhageni* differs from *B. kashmirensis* s.str. principally in that the pale pubescence is entirely yellow (resembling Fig. 295), rather than both white and yellow (Fig. 302). The male genitalia of the bees of this group from Kashmir show limited variation, although this is more pronounced in the shape of the gonostylus (Figs 181–183). The apex of the gonostylus is formed from a thin plate, which has an irregular margin. The variation in the extent of this plate is not associated with the variation in colour pattern and appears to be of only individual significance. The yellow males are otherwise closely similar to those of *B. kashmirensis* s.str., even in the size and shape of their eyes. All of the workers collected at Gumri near the Zoji La in the Great Himalaya range are intermediate between the *B. mastrucatus* subsp. *meinertzhageni* of Ladakh and the *B. kashmirensis* s.str. from the mountains around the Vale of Kashmir in that they have the pale pubescence of the thorax grey-white and that of both abdominal terga I-II bright yellow (Fig. 301).

Skorikov described females from Sichuan that have the pale pubescence reduced to a few grey-cream hairs mixed with the black pubescence on the anterior thoracic dorsum under the name *Alpigenobombus beresovskii*. The pattern of punctures on the female clypeus does not associate them definitely with either *B. wurflenii* or *B. kashmirensis*, but Skorikov's description of the male genitalia (Skorikov, 1933*b*: 248) agrees more closely with *B. kashmirensis*. From the meagre evidence available at present, I consider that *Alpigenobombus beresovskii* is most likely to be part of the same species as *B. kashmirensis*.

DISTRIBUTION. *B. kashmirensis* is primarily a Tibetan species (Map 31). It is known from Gansu (Morawitz, 1880; Bischoff, 1936; PW, ZS), Qinghai (Morawitz, 1886; Bischoff, 1936; Wang, 1982; PW, ZS), Sichuan (Morawitz, 1890; Skorikov, 1933*b*; Wang, 1982; ZI), Guangxi [no precise locality cited] (Wang, 1982), Tibet (Richards, 1930; Wang, 1982; BMNH, PW), Nepal (Tkalců, 1974*b*; NMS), Uttar Pradesh (BMNH), Himachal Pradesh (BMNH, PW) and Kashmir. A record from Mongolia (MNHU) needs to be confirmed.

MATERIAL EXAMINED FROM KASHMIR. *B. kashmirensis* is widespread in Kashmir, recorded from the Hindu Raj, Ladakh, Zanskar, Great Himalaya and Pir Panjal ranges, in alpine scrub and steppe (Map 32, Fig. 6): 34 queens, 172 workers, 67 males, from 15 localities 2400–4800 m (BMNH, FA, ITZ, MI, MNHN, MNHU, NR, PW, TL; 1 worker photographed in the Sangisfaid valley, C. A. Chadwell).

A colony was found at the western end of Nimaling plain (4800 m, 15.vii.1980). The entrance to the nest was under a 2 m boulder in the derelict terminal moraine.

VARIATION WITHIN KASHMIR. Individuals from the Ladakh and Zanskar ranges have the pale pubescence yellow, with only a narrow band of black hairs basally on tergum III (Figs 295–300). The pubescence of terga III-VI is orange-red, with at most only a few hairs of terga V-VI pale-tipped.

Workers from Gumri in the Great Himalaya range are similar, but the pale hairs of the thorax are grey-white rather than yellow (terga I-II yellow, or 1/4 workers with some grey-white hair antero-laterally on tergum I) and the orange-red hairs of terga IV-VI are white-tipped (Fig. 301). Males and females from the Hindu Raj range are similar, but the pale hairs of tergum I are also grey-white (tergum II yellow). Material from around the Kishanganga valley includes individuals with both yellow and white pubescence (4/10 queens, 16/123 workers, 10/43 males), and some individuals for which the yellow is completely replaced by white, even on tergum II (6/10 queens, 107/123 workers, 33/43 males). On Mt Apharwat in the Pir Panjal range, the yellow and white individuals predominate (9/10 queens, 24/27 workers, 16/17 males). Another worker from Apharwat has very few pale hairs on the thorax and many black hairs intermixed on terga I-III (cf. *B. beresovskii*). The yellow and white individuals usually have a distinct black band at the base of tergum III that may extend over most of tergum III for queens and males (Figs 302–304). These queens have the yellow very pale and the white-tipped hairs of terga III-VI are only orange-red at their bases. In contrast, the white individuals often have few black hairs on tergum III, the hairs of terga III-VI are often completely orange-red and the white pubescence at the rear of the thorax may be almost completely replaced by black hairs (Figs 305–310).

The yellow individuals of this species (Figs 295–300) from Ladakh are closely similar in colour pattern to *B. oberti* (Figs 392 & 393), which is known to occur with them. These individuals may also resemble some of the *B. himalayanus* (Figs 242 & 243) and *B. ladakhensis* (Figs 394 & 396) that occur with them. *B. kashmirensis* can be recognised by its 6-toothed mandibles (Fig. 32). The white and yellow individuals (Figs 302–304) from the mountains around the Vale of Kashmir are particularly closely similar in colour pattern to the *B. rufofasciatus* (Figs 434–436, 438, 439) that occur with them. *B. kashmirensis* can be recognised by the longer and white-tipped, red hairs on terga III-VI, where the hairs of *B. rufofasciatus* are short and either red or white. These individuals may also resemble some *B. himalayanus* (Figs 244–252), *B. novus* males (Figs 260 & 262), *B. lemniscatus* (Figs 325 & 326), *B. lepidus* (Figs 330, 331, 333, 334) and *B. biroi* (Figs 338 & 339). The white individuals of this species (Figs 305–310) from the mountains around the Kishanganga valley and the Vale of Kashmir are particularly closely similar in colour pattern to some of the *B. biroi* (Figs 341 & 342) that occur with them at some localities. These individuals may also resemble some *B. avinoviellus* (Figs 238–241), *B. himalayanus* (Figs 250–252), *B. tunicatus* (Figs 350, 353, 355), *B. asiaticus* (Figs 386 & 387) and *B. keriensis* (Figs 408 & 409). *B. kashmirensis* is easily recognised by its 6-toothed mandibles (Fig. 32).

FOOD PLANTS. **Kashmir**: (Ranunculaceae) *Aconitum laeve* Royle, *A. heterophyllum* Wallich ex Royle, *A. hookeri* Stapf, *A. violaceum* Jacquem. ex Stapf; (Compositae) *Lactuca lessertiana* (DC.) C. B. Clarke, unidentified dandelion-like composites; (Gentianaceae) *Swertia petiolata* D. Don; (Scropulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced], *Pedicularis oederi* Vahl, *P. pectinata* Wallich ex Benth., *P. punctata* Decne.

Ladakh: (Leguminosae) *Caragana versicolor* (Wallich) ex Benth.; (Labiateae) *Stachys tibetica* Vatke.

Subgenus ***PYROBOMBUS*** Dalla Torre

Pyrobombus Dalla Torre, 1880: 40 (as a subgenus of *Bombus* Latreille). Type species: *Apis hypnorum* Linnaeus, 1758: 579 = *Bombus hypnorum* (Linnaeus), by monotypy.

Poecilobombus Dalla Torre, 1882: 23 (as a subgenus of *Bombus* Latreille). Type species: *Bombus sitkensis* Nylander, 1848: 235, by subsequent designation of Sandhouse (1943: 589). Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

[*Pyrrhobombus* Dalla Torre; Dalla Torre, 1882: 28 (as a subgenus of *Bombus* Latreille). Incorrect subsequent spelling, unavailable name (Art. 33c).]

Pyrrhobombus Dalla Torre; Dalla Torre, 1896: 503 (as a subgenus of *Bombus* Latreille). Unjustified emendation (Art. 33b(i, iii)).

Pratobombus Vogt, 1911: 49 (as a subgenus of *Bombus* Latreille). Type species: *Apis pratorum* Linnaeus, 1761: 424 = *Bombus pratorum* (Linnaeus), by subsequent designation of Frison (1927: 67). Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

Anodontobombus Krüger, 1917: 61, 65 (as a subgenus of *Bombus* Latreille). Type species: *Apis hypnorum* Linnaeus, 1758: 579 = *Bombus hypnorum* (Linnaeus), by present designation (see Note below). Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

Uncobombus Vogt *in* Krüger, 1917: 65 (as a subgenus of *Bombus* Latreille). Type species: *Apis hypnorum* Linnaeus, 1758: 579 = *Bombus hypnorum* (Linnaeus), by present designation (see Note below). Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

Lapponicobombus Quilis-Pérez, 1927: 19 (as a subgenus of *Bombus* Latreille). Type species: *Apis lapponica* Fabricius, 1793: 318 = *Bombus lapponicus* (Fabricius), by subsequent designation of Milliron (1961). Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

[*Hypnorubombus* Quilis-Pérez, 1927: 19 (as a subgenus of *Bombus* Latreille). Incorrect original spelling (Art. 32c(iv)), unavailable name (Art. 19a).]

[*Laponicobombus* Quilis-Pérez, 1927: 63 (as a subgenus of *Bombus* Latreille). Incorrect original spelling (Art. 32c(iv)), unavailable name (Art. 19a).]

Hypnorobombus Quilis-Pérez, 1927: 97 (as a subgenus of *Bombus* Latreille). Type species: *Apis hypnorum* Linnaeus, 1758: 579 = *Bombus hypnorum* (Linnaeus), by monotypy. Synonymised with *Pyrobombus* Dalla Torre by Milliron (1961).

Pratibombus Vogt; Skorikov, 1938*a*: 146. Unjustified emendation (Art. 33b(i, iii)).

Note. The names *Anodontobombus* Krüger and *Uncobombus* Vogt were originally proposed for a section of the genus *Bombus* and a group of subgenera respectively, but they must both be treated as subgeneric names (Art. 10e). Milliron (1961: 53) considered *Anodontobombus* Krüger to be synonymous with his concept of the subgenus *Pyrobombus* Dalla Torre (within his genus *Pyrobombus* Dalla Torre). Milliron also considered *Uncobombus* Vogt to 'correspond' to *Pyrobombus* Dalla Torre. The type species of both subgenera are designated as *Apis hypnorum* Linnaeus, in common with *Pyrobombus* Dalla Torre, in order to stabilise an unnecessarily complex nomenclature.

For a general description of both sexes see Richards (1968). His descriptions include many exceptions for the characters of *B. festivus* Smith, which was subsequently placed in a separate subgenus *Festivobombus* by Tkalců (1972).

Bombus (Pyrobombus) hypnorum (Linnaeus)

(Figs 64, 104, 144, 184, 311–316, Maps 33 & 34)

Apis hypnorum Linnaeus, 1758: 579. Lectotype queen by designation of Day (1979: 64), SWEDEN: no further data (LSL) [examined].

[*Bombus hypcorum* (Linnaeus); Walckenaer, 1802: 148. Incorrect subsequent spelling, unavailable name (Art. 33c).]

Bombus (Pratobombus) hypnorum var. *bryorum* Richards, 1930: 650 (see Note below). Holotype queen [not the male] by original designation [p. 651], INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (BMNH) [examined]. **Syn. n.**

Bombus fletcheri Richards, 1934: 90. Holotype queen by original designation, INDIA: Kashmir, Gulmarg, 7.vi.1931 (*Fletcher*) (BMNH) [examined]. **Syn. n.**

Pyrobombus (Pyrobombus) bryorum (Richards); Tkalců, 1974*b*: 328.

NOMENCLATURE. Note. Richards's use (1930: 634 etc.) of the term 'Subsp.' elsewhere in his paper could be taken to indicate that infrasubspecific rank is meant for *B. hypnorum* var. *bryorum*, although his comment 'this Indian form' does associate the nominal taxon with a particular geographical area (Art. 45f(ii)). However, this has subsequently been treated as a name in the species group by Tkalců (1974*b*), so Richards's taxon is therefore deemed to be of subspecific status (Art. 45g(ii)(1)).

AFFINITIES. Species of the subgenus *Pyrobombus* share a reduction and ventral displacement of the interio-basal process of the male gonostylus, with an apically-directed extension that forms a longitudinal ridge, just ventral and parallel to the inner margin of the gonostylus (Figs 184–191) (synapomorphy). An intermediate form of this structure may be seen in the gonostylus of *B. (Festivobombus) festivus* Smith, which has the interio-basal process only partially reduced and rotated ventrally, but with a weakly sclerotised fold running apically, below the inner margin of the gonostylus. The subgenus *Pyrobombus* has more species (at least 42) than any other subgenus of bumble bees and many of these species are morphologically closely similar. Consequently ideas of the relationships among the species are at present particularly tentative.

Himalayan *B. hypnorum* have often been confused with the workers of *B. (Festivobombus) festivus*, which have a similar colour pattern. *B. festivus* is common in southern China and the eastern Himalaya to as far west as Himachal Pradesh (BMNH, PW, UM). It may also be present in the foothills of south-eastern Kashmir (unconfirmed record by Skorikov, 1933*b*). The workers of *B. festivus* have the disto-posterior angle of the hind tibia spinosely produced, whereas for *B. hypnorum* this process is no longer than broad. The pubescence of *B. festivus* is generally shorter and more even, with a particularly dense covering of short, branched hairs on the head, posterior to the eyes. The male genitalia of *B. festivus* show similarities to those of *B. hypnorum*, but have a distinct interio-basal process of the gonostylus (see Tkalců, 1974*b*: fig. 114), lack a well-defined ventro-basal angle of the penis valve (see the comments on *B. asiaticus*), and have the volsella strongly constricted just before its apex.

Within the subgenus *Pyrobombus*, the rare *B. abnormis* (Tkalců) from Sikkim (Tkalců, 1968*a*; BMNH) also resembles *B. hypnorum* in colour pattern, but with fewer pale hairs on the apical terga. The ocello-ocular area is, however, almost completely and densely covered with fine punctures for both sexes of *B. abnormis*. The male genitalia differ from those of *B. hypnorum* in that the volsella is weakly, but distinctly, constricted before its apex (more like *B. festivus*), of which the outer corner is acute, and the recurved hook of the penis valve head is shorter than for *B. hypnorum* (more like *B. festivus*). The interio-apical angle of the gonocoxite of *B. abnormis* is broadly rounded, rather than acutely pointed, and the shape of the gonostylus differs (see Tkalců, 1968*a*: fig. 52–56).

B. hypnorum may be one of the most plesiomorphic species of the subgenus *Pyrobombus*, at least insofar as the the gonostylus retains a well-defined inner basal notch (Fig. 184) and the recurved hook of the penis valve head remains broad but narrowed to a rounded point (Fig. 64). At present I am not aware of any synapomorphic characters from which to recognise a monophyletic '*hypnorum*-group' (cf. the '*hypnorum*-Gruppe' of Tkalců, 1968*a*, 1989). Many other Old World species of the subgenus *Pyrobombus* have the recurved hook broadened apically and more spatula-shaped (e.g. the *pratorum*-group, see the comments on *B. biroi*, Figs 70 & 71), or more or less shortened (e.g. the *parthenius*-group, see the comments on *B. lepidus*, Figs 67 & 68).

B. hypnorum is closely similar to the North American *B. perplexus* Cresson. In the Old World, its closest relative may be *B. haematurus* Kriechbaumer, which is known from south-eastern Europe, Turkey and the Caspian coast of Iran (D. B. Baker, pers. comm.; BMNH, PW). Females of *B. haematurus* have the posterior half of the thoracic dorsum and tergum I black-haired and the post ocello-ocular area is more smooth and more finely punctured than for *B. hypnorum*. The distal margin of the male gonocoxite is more nearly at a right angle to its longitudinal axis for *B. haematurus* (se Krüger, 1943: p. 540 figs 1–12) and the gonostylus is shorter than for *B. hypnorum* (see Krüger, 1943: p. 538 figs 1–7).

B. hypnorum appears to be widespread between northern Europe and Kashmir. Both females and males differ slightly in colour pattern between the two regions (by extension of the area of pale pubescence onto at least tergum II among individuals from Asia; see Reinig, 1939: fig. 8). Individuals from the Himalaya have been regarded as a separate species, *B. bryorum*, by Tkalců (1974*b*), although I can find no reliable morphological differences. The queen described under the name *B. fletcheri* by Richards is closely similar to other faded queens of *B. hypnorum* from Gulmarg. Individuals of all of these nominal taxa occupy similar habitats in the upper montane coniferous forest. The males search for mates by patrolling the forest in a similar way and I know of no evidence to suggest that individuals from Kashmir would not interbreed with those from Europe if they were to occur on the same mountain (cf. comments on *B. asiaticus*, *B. rufofasciatus* and *B. kashmirensis*). Therefore they are all considered to be parts of the same species.

DISTRIBUTION. *B. hypnorum* is widespread in the Old World (Map 33). It is known from Europe (but not Britain e.g. Reinig, 1939; Løken, 1973) and eastwards across the U.S.S.R. (Reinig, 1939; Panfilov, 1984; BMNH) to as far as Kamchatka (Bischoff, 1930; Reinig, 1939; BMNH) and Hokkaido in Japan (Tkalců, 1965; Sakagami & Ishikawa, 1969; BMNH, PW). In central Asia it reaches southwards to the Caucasus and the Altai (Panfilov, 1984) and Mongolia (Skorikov, 1931, 1933*a*; Reinig, 1939; PW); and in the south-east it is recorded from North Korea (Kim & Ito, 1987), Gansu (Bischoff, 1936; Reinig, 1939), Sichuan (Morawitz, 1890), Yunnan (Wang, 1987), Burma and Arunachal Pradesh (BMNH), Tibet (Richards, 1930; Wang, 1987), Sikkim (Friese, 1918), Nepal (Tkalců, 1974*b*; BMNH, NMS) and Kashmir. Part of this distribution is mapped by Reinig (1939: fig. 8) and also by Panfilov (1984: map 186).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. hypnorum* is recorded from the Hindu Raj range, from the southern side of the Great Himalaya range and from the Pir Panjal range, in the upper montane coniferous forest (Map 34, Fig. 6): 6 queens, 43 workers, 22 males, from 5 localities 2400–3700 m (BMNH, NR, PW).

VARIATION WITHIN KASHMIR. The colour pattern of the females resembles that of individuals from northern Asia, in that pale brown hairs often cover most of tergum II (Figs 311, 314, 315). Most workers have some pale hairs intermixed on tergum III as well, and extreme workers from Mt Apharwat have just a few black hairs intermixed on terga III-IV (Fig. 312, 5/26 workers). On the thorax the pale brown pubescence extends down to the leg bases and femora in most individuals.

The males are much lighter in colour pattern than those from Europe (but see the discussion of the colour patterns of the Kashmir fauna). Their pubescence is almost uniformly lemon yellow, with the exception of a few black hairs intermixed on the head and on terga IV-V, and of white hairs on terga V-VII (Figs 313 & 316).

Females of this species are distinctive in their appearance. The yellow males with white hairs on the apical terga (Figs 313 & 316) may be similar in colour pattern to the males of *B. lucorum* (Figs 365 & 370), which occur with them at some localities. *B. hypnorum* males can be recognised by their smaller size and by the inwardly hooked apices of the penis valves (Fig. 64).

HOST PLANTS. (Ranunculaceae) *Cimicifuga foetida* L., *Aconitum laeve* Royle; (Balsaminaceae) *Impatiens glandulifera* Royle, unidentified small yellow balsam; (Sambucaceae) *Lonicera quinquelocularis* Hardw.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC.; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced]; (Labiateae) *Prunella vulgaris* L., *Salvia hians* Royle ex Benth.

Bombus (Pyrobombus) subtypicus (Skorikov), comb. n.

(Figs 41, 65, 66, 105, 106, 145, 146, 185, 186, 216, 317–324, Maps 35 & 36)

Bombus leucopygus Morawitz *in* Fedtschenko, 1875: 3. Lectotype female by designation of Skorikov (1914*c*: 293) (see Note 2 below), U.S.S.R.: Tadzhikistan S.S.R. or Uzbekistan S.S.R. (ZI) [not seen]. Junior primary homonym of *Bombus leucopygus* Illiger, 1806 [= *B. hypnorum* (Linnaeus)].

[*Pratobombus leucopygos* Skorikov, 1914*c*: 293. Incorrect subsequent spelling, unavailable name (Art. 33c).]

Pratobombus leucopygos var. *subtypicus* Skorikov, 1914*c*: 294. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, U.S.S.R.: ?Uzbekistan S.S.R., 'Bukan-Khapa', 27.v.1911 (*Topbek*) (ZI) [examined].

Bombus leucurus Bischoff & Hedicke, 1931: 391. Unnecessary replacement name for *B. leucopygus* Morawitz. Synonymised with *Pyrobombus subtypicus* (Skorikov) by Tkalců (1968*a*).

Pyrobombus (Pyrobombus) subtypicus (Skorikov); Tkalců, 1968*a*: 27 (see Note 1 below).

Pyrobombus (Pyrobombus) kohistanensis Tkalců, 1989: 49. Holotype queen by original designation, PAKISTAN: Indus Kohistan, Kagan valley, Naran, 2400–3000 m, 3–13.vi.1977 (*de Freina*) (ZS) [examined]. **Syn. n.**

NOMENCLATURE. Note 1. *Bombus subtypicus* (Skorikov) replaces *Bombus leucopygus* Morawitz because it is the oldest available name (Art. 60b) (Tkalců, 1968*a*, 1969*a*).

TYPE MATERIAL. Note 2. Skorikov (1914*c*) described the variation among Morawitz's syntypes of *B. leucopygus* in the ZMMU. He stated that he considered that the first specimen bearing a large label with the name of the species was the type. This use of the word type in reference to a single specimen is taken to be a valid lectotype designation (Art. 74b).

AFFINITIES. Within the subgenus *Pyrobombus* (see the comments on *B. hypnorum*), close relatives of *B. subtypicus*, as judged from the similarity in the form of the male genitalia, may include both *B. haematurus* and *B. lemniscatus* (see the comments on *B. hypnorum* and *B. lemniscatus*). However, for *B. subtypicus* the recurved hook of the penis valve head is more acutely pointed (Figs 65 & 66) than for either of the other two species (e.g. Fig. 67) (see Krüger, 1943: p. 541 figs 1–11). Unlike *B. haematurus*, *B. subtypicus* has virtually no interio-basal notch on the gonostylus above the interio-apical corner of the gonocoxite near their point of contact (Figs 185 & 186). The females of *B. haematurus* can be distinguished by their long pubescence and by their many close and regular fine punctures in the post ocello-ocular area of the head.

Skorikov (1914*c*) described the local variation in the colour pattern of the pubescence among Morawitz's series of *B. leucopygus* Morawitz from 'Turkestan'. Some of these individuals had the black band between the wing bases partially or completely replaced by yellow pubescence.

Recently Tkalců (1989) described a single queen under the name *Pyrobombus kohistanensis* from across the Pakistan border in the Indus-Kohistan range that has a colour pattern similar to the banded grey-white individuals of *B. avinoviellus*. This specimen (Tkalců, 1989: figs 14, 18, 22) is closely similar in morphology to *B. subtypicus* and is likely to be part of the same species. It differs from individuals of *B. subtypicus* from Kashmir that have a black band between the wings principally in that the pale pubescence is nearly white, rather than yellow. However, a single queen from nearby on the Kashmir side of the border at Astor is intermediate in these characters insofar as it has both black hairs intermixed between the wing bases and the pale pubescence is a particularly pale yellow. More specimens, especially of the males, are needed in order to establish definitively the relationships of this nominal taxon.

DISTRIBUTION. *B. subtypicus* is a central Asian species (Map 35). It is known from the Tien Shan (Morawitz, 1880; Skorikov, 1914*c*, 1931; Krüger, 1943; BMNH, ZI), the Pamir (Reinig 1930, 1934; Skorikov, 1931; BMNH), the Hindu Kush (Reinig, 1934, 1940; Richards, 1951; Tkalců, 1969*a*; BMNH, PW), Pakistan (Tkalců, 1989; BMNH, PW, ZS) and Kashmir. The record from Gansu (Bischoff, 1936) is based on a misidentification (Tkalců, 1968*a*).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. subtypicus* is recorded from the Hindu Raj range and from the Great Himalaya range, in dry subalpine scrub (Map 36): 2 queens, 36 workers, 108 males, from 9 localities 2700–3700 m (BMNH, NR, PW).

A colony was found near Dras (3200 m, 10.viii. 1986). The nest entrance was at the base of a dry-stone wall.

VARIATION WITHIN KASHMIR. Material from Kashmir is relatively homogeneous in colour pattern, at least insofar as all specimens have the pubescence of the apical terga orange-red rather than white (Figs 317–324). Females from the Hindu Raj range and from Matayan and Dras in the Great Himalaya range have yellow hairs on the head and to a more variable extent on terga I-II (Figs 319, 320, 323). These individuals have only a few black hairs on the thoracic dorsum.

The single queen from Astor has the head, the ventral parts of the thorax and terga I-II black (Fig. 322). Black hairs are also more numerous between the wing bases, where they form an indistinct band. The yellow pubescence of this individual is particularly pale.

The single worker from Lal Pani has a broad, black band between the wing bases (Fig. 317). The hairs of its head are black but those of terga I-II are yellow. Some of the males from the same locality also have a black band between the wing bases (Fig. 318, 10/25 males).

The individuals of this species that lack a black band between the wing bases (Figs 319–324) are closely similar to some *B. biroi* (Figs 335–337), although they are not known to occur together. They are also similar to some of the *B. avinoviellus* (Fig. 232), *B. marussinus* (Figs 254–257), *B. branickii* (Fig. 265), *B. asiaticus* (Figs 371–376) and *B. semenovianus* (Figs 397–402) that may occur with them at some localities. Unbanded *B. subtypicus* can be recognised by the characters given in the key (couplets 19 & 20). The individuals with the black thoracic band (Figs 317 & 318) resemble some of the *B. avinoviellus* (Figs 233–235), *B. asiaticus* (Figs 377 & 378) and *B. keriensis* (Fig. 414–416) that occur with them. *B. subtypicus* can be recognised by its small size, by its shiny outer surface to the hind tibia, and by the small number of fine punctures in the ocello-ocular area of the head (Fig. 216).

FOOD PLANTS. (Leguminosae) *Melilotus officinalis* (L.) Pallas, *Trifolium repens* L.; (Scrophulariaceae) *Verbascum thapsus* L.; (Labiateae) *Nepeta podostachys* Benth., *Prunella vulgaris* L.

Bombus (Pyrobombus) lemniscatus Skorikov

(Figs 15, 67, 107, 147, 187, 212, 218, 223, 325, 326, Maps 37 & 38)

Bombus lemniscatus Skorikov, 1912*b*: 606. Holotype queen by monotypy, CHINA: Qinghai, northern slopes of the Xining mountains, 30.v. 1890 (*Grum-Grzhimailo*) (ZI) [examined].

Bombus nursei var. *flavopilosus* Friese, 1918: 84. LECTOTYPE queen by present designation (see the Note below), no data (*Bingham*) (MNHU) [examined]. **Syn. n.**

Bombus (Lapidariobombus) peralpinus Richards, 1930: 646. Holotype queen [not a worker] by original designation [p. 647], CHINA: Xizang [= Tibet], Rongshar valley, Tasam, 12000 ft [3700 m], 20.vi.1924 (*Hingston*) (BMNH) [examined]. Synonymised with *Pyrobombus lemniscatus* (Skorikov) by Tkalců (1974*b*).

TYPE MATERIAL. Note. Tkalců (1968*a*) described *Pyrobombus mirus* from a queen that is the only one of Friese's three syntype queens of *B. nursei* var. *flavopilosus* to bear one of the red 'Type' labels. Tkalců (1968*a*: 39) had noted that there are some discrepancies between this individual and Friese's original description, but contrary to Tkalců's conclusion ('kann infolge der Nachtübereinstimmung mit der Urbeschreibung nicht die Lectotype dieses Taxons [*B. nursei* var. *flavopilosus*] darstellen'), this does not prevent this specimen from being a syntype (Art. 73b), so it remains a candidate for designation as the lectotype of *B. nursei* var. *flavopilosus*. However, another one of Friese's syntypes is designated here as lectotype of *B. nursei* var. *flavopilosus* in order to maintain the current usage of the name *B. mirus* (Tkalců). A queen in the MNHU collection agrees with the original description of *B. nursei* var. *flavopilosus* and carries a label (1) 'Coll. Bingham'; (2) '*B. nursei* / *flavopilosus* / [female] 1914 Friese det. / Fr.'; (3) a red printed label 'Paratypus'; (4) 'LECTOTYPUS / *B. nursei var.* / *flavopilosus* / Friese Tkalců det [female]' [designation not published]. This specimen, which is badly damaged with *Anthrenus* holes and lacks the left front tarsi and the right mid and hind tarsi, is designated as lectotype (Art. 74a).

AFFINITIES. Within the subgenus *Pyrobombus* (see the comments on *B. hypnorum*), *B. lemniscatus* is likely to be related to the *parthenius*-group of species. All other species of this group, with the possible exception of *B. mirus* (Tkalců), have the ventro-basal angle of the penis valve displaced closer to the penis valve apex than to its base (Figs 107–109), with the shoulder between this angle and the base of the penis valve head strongly curved, and the head of the penis valve broadened basally (Figs 67–69, 107–109) (synapomorphies). This group includes Tkalců's (1974*b*, 1989) '*parthenius*-Gruppe' together with the additional species *B. lepidus*, *B. infirmus* (Tkalců) and probably *B. lemniscatus* and *B. mirus* (see the comments on *B. lepidus*).

There are two more-distantly related species of the subgenus *Pyrobombus* that occur at lower altitudes in the eastern Himalaya, to at least as far west as Uttar Pradesh (BMNH): *B. rotundiceps* Friese and *B. flavescens*. It is possible that *B. rotundiceps* may also be present in Kashmir (unconfirmed record by Skorikov, 1933*b*). This species closely resembles the local *B. trifasciatus* and *B. haemorrhoidalis* in the colour pattern of the pubescence (see the comments on those species). Females of both *B. rotundiceps* and *B. flavescens* from Uttar Pradesh have the pubescence of the thoracic dorsum entirely black. The legs are extensively bright orange-brown for *B. flavescens* but black for *B. rotundiceps*.

Another Himalayan species, which resembles *B. lemniscatus* more closely and which may belong to the *parthenius*-group in its broadest sense, is *B. mirus*. Females of *B. mirus* have a colour pattern similar to some of the darker, white *B. biroi* from Kashmir (Fig. 341), but with the pubescence of tergum III predominantly black. They can be distinguished from most species by the profuse punctures that cover more than half of the ocello-ocular area of the head (though not as extensive as for *B. abnormis*, see the comments on *B. hypnorum*). Females of *B. mirus* are known from the alpine zone of Nepal (BMNH, PW), Sikkim (Tkalců, 1968*a*; BMNH, MNHU) and Tibet (Wang, 1982). Wang also described a male from Zayü in Tibet (not seen). This male is apparently similar in its genitalia (Wang, 1982: fig. 32) and in its white and yellow colour pattern to another male from Tibet described by Friese (1913) under the name *B. pratorum* var. *tibetanus* (junior secondary homonym in *Bombus* of *Apathus tibetanus* Morawitz). The genitalia of both appear to differ from those of *B. lemniscatus* primarily in their strongly concave interior margin of the gonostylus.

B. lemniscatus (redescribed independently under the name *B. nursei* var. *flavopilosus* by Friese, see the Note above, and under the name *B. peralpinus* by Richards) is closely similar to *B. lepidus* not only in morphology, but also in the colour pattern of the pubescence and in its distribution. Skorikov (1912*b*) distinguished females of *B. lemniscatus* by their longer pubescence, slightly longer oculo-malar distance, more sharply defined band of black hairs between the wing bases and by their generally more extensive black pubescence. Tkalců has listed several other subtle differences between the females (Tkalců, 1989: table 3) and noted that the scutum, on the thoracic dorsum, is punctured almost throughout for *B. lemniscatus* (Fig. 223) but broadly unpunctured in the middle for *B. lepidus* (Fig. 224). A single male in the BMNH collection from 'Rata, 11,000 ft.' [= 3350 m], Uttar Pradesh, shows similar hair length, colour pattern and sculpture of the scutum to females of *B. lemniscatus*. Although the genitalia of this male are closely similar to those of *B. lepidus*, they do differ in that, unlike *B. lepidus* from Kashmir, the recurved head of the penis valve is slightly narrower (Fig. 67), the ventro-basal angle of the penis valve is just closer to the base of the penis valve shaft than to the penis valve head (Fig. 107), and the interio-apical process of the volsella is broader and extends without a concave angle to the exterio-apical corner of the volsella (Fig. 147). All of the available males of *B. lepidus* can be distinguished by their extensively yellow colour pattern of the pubescence, which has few white or black hairs (see the discussion of convergent colour patterns). More material, especially of the males, of *B. mirus*, *B. lemniscatus* and *B. lepidus* is needed from Nepal, where all three species may occur in proximity, in order to clarify their relationships.

DISTRIBUTION. *B. lemniscatus* is primarily a Tibetan species (Map 37). It is known from Gansu (Bischoff, 1936), Qinghai (Skorikov, 1912*b*; PW, ZI, ZS), Sichuan (BMNH, PW), Tibet (Richards, 1930; Wang, 1982, 1988; BMNH), Sikkim (BMNH, MNHU), Nepal and Uttar Pradesh (BMNH) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. lemniscatus* is recorded only from Mt Apharwat in the Pir Panjal range, from above the montane coniferous forest (Map 38): 2 workers, Apharwat, above 3000 m, viii–ix.1986 (*Williams*) (PW).

VARIATION WITHIN KASHMIR. The workers from Mt Apharwat differ from one another in the extent of the pale pubescence on the scutellum, at the rear of the thoracic dorsum, and on tergum III (Figs 325 & 326).

This species is particularly closely similar in colour pattern to some of the white and yellow *B. lepidus* (Figs 330 & 334) and *B. biroi* (Figs 338 & 339) that occur with it. They also resemble some of the *B. himalayanus* (Figs 247–252), *B. novus* males (Figs 260 & 262), *B. kashmirensis* (Figs 302–304) and *B. rufofasciatus* (Figs 434–436, 438, 439) from the same area. *B. lemniscatus* can be recognised by the combination of the dense patch of small punctures in the ocello-ocular area of the head (Fig. 218) together with the very narrowly unpunctured median area of the thoracic scutum (Fig. 223; see the key, couplets 19 & 21).

FOOD PLANTS. No records.

Bombus (Pyrobombus) lepidus Skorikov

(Figs 68, 69, 108, 109, 148, 149, 188, 189, 213, 219, 224, 327–334, Maps 39 & 40)

Bombus lepidus Skorikov, 1912*b*: 606. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, CHINA: Qinghai, northern slopes of the Xining mountains, 30.v. 1890 (*Grum-Grzhimailo*) (ZI) [examined].

Bombus genitalis Friese, 1913: 85. Holotype male by monotypy (see Note 1 below), CHINA: Tibet, no further data (*Staudinger*) (MNHU) [examined]. **Syn. n.**

Bombus nursei var. *tetrachromus* Friese, 1918: 85. LECTOTYPE queen by present designation (see Note 2 below), INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (MNHU) [examined]. Junior primary homonym of *Bombus tetrachromus* Cockerell, 1909 [= *B. kashmirensis* Friese]. **Syn. n.**

Bombus (Pratobombus) yuennanicola Bischoff, 1936: 7. Holotype queen by original designation, CHINA: Yunnan, Lijiang, 15.v.1934 (*Höne*) (MNHU) [examined]. Change of status to *Pyrobombus lepidus* subsp. *yuennanicola* (Bischoff) by Tkalců (1989). Provisional synonym.

Bombus (Pyrobombus) yunnanicola Bischoff; Wang, 1982: 435. Unjustified emendation (Art. 33b(i, iii)).

Pyrobombus (Pyrobombus) lepidus subsp. *hilaris* Tkalců, 1989: 48. Holotype queen by original designation, PAKISTAN: Gilgit, Banidas, 36°11′N 74°33′E, 2600 m, 30.vi–2.vii.1959 (*Lobbichler*) (ZS) [examined]. **Syn. n.**

TYPE MATERIAL. Note 1. Friese's description of *B. genitalis* specifies that only a single male was examined. A single male in the MNHU collection agrees with the original description and carries the data quoted, together with a red printed label 'Type', and one of Friese's determination labels 'Bombus / genitalis / [male] 1912 Friese det / n. Fr.'. This is believed to be the single individual on which the original description is based and is regarded as the holotype.

Note 2. Friese's description of *B. nursei* var. *tetrachromus* lists two queens. A single queen in the MNHU collection agrees with the original description and carries a label (1) 'Kashmir / 8–9000ft / 6.01'; (2) 'Bombus / tetrachromus / [female] 1915 Friese det. / Fr.'; (3) a red printed label 'Type'. This specimen, which lacks both front tarsi and the mid left tarsus, is designated as lectotype (Art. 74a).

AFFINITIES. Within the subgenus *Pyrobombus* (see the comments on *B. hypnorum*), *B. lepidus* belongs to the *parthenius*-group of species (see the comments on *B. lemniscatus*).

Within the *parthenius*-group, the recurved hook of the penis valve head remains broad and scarcely shortened for males of *B. lepidus* (Figs 68 & 69) (plesiomorphy within the *parthenius*-group), although males of most of the other species have the recurved hook much shortened (synapomorphy of *B. infirmus* + *B. parthenius* + *B. luteipes*). Individuals of *B. infirmus* (Tkalců) are banded with yellow pubescence like individuals of *B. lucorum*, but have fewer white hairs on the apical terga. *B. infirmus* is known from northern Burma (BMNH) and Sichuan (BMNH, PW). Females of the two Himalayan species, *B. parthenius* Richards (14.iv.1934) (which is probably conspecific with *Bremus sonani* Frison, 30.iv.1934) and *B. luteipes* Richards (conspecific with *Pyrobombus signifer* Tkalců, 1989, **syn. n.**), can be recognised by their generally dull grey-yellow pubescence (lighter for the males), with no distinct black band between the wing bases. The apical parts of the sterna and the distal sclerites of the legs are usually a lighter orange-brown colour for females of *B. luteipes* (see Tkalců, 1989: fig. 26) than for females of *B. parthenius*. Males of *B. luteipes* have very distinctive large genitalia, which have the interio-apical corner of the gonocoxite spinosely produced rather than forming a right angle as for *B. parthenius*. *B. luteipes* and *B. parthenius* are known from China and the eastern Himalaya to as far west as Nepal (BMNH, NMS, PW) and Uttar Pradesh (BMNH). Individuals of *B. parthenius* tend to occur at higher altitudes in the montane forests than do those of *B. luteipes*.

Another nominal taxon, *Pyrobombus infrequens*, has been described recently (Tkalců, 1989) from four workers from Burma and China. These are similar to workers of *B. parthenius*, but the oculo-malar distance is described as slightly longer. Other workers from near Gongga Shan in Sichuan (PW) are similar to the holotype of *Pyrobombus infrequens* in that they have few large punctures near the middle of the clypeus, although these workers have most of the orange-red pubescence of terga IV-V replaced by black. A male from the same locality also differs from Nepalese *B. parthenius* in that the orange-red pubescence of terga IV-V is replaced by black.

The genitalia of this male are closely similar to those of males from Nepal, although the gonostylus projects inwards distinctly beyond the interio-apical corner of the gonocoxite, whereas this corner of the gonocoxite is longer for both *B. parthenius* and *B. luteipes*, and the volsella is slightly broader from the ventral aspect. Much more material of the nominal taxa of the *parthenius*-group is required to establish their relationships definitively.

Most females of *B. lepidus* from Kashmir have the pale bands of the thoracic pubescence grey-white and have relatively few black hairs on the gastral terga (e.g. Fig. 333; redescribed independently under the name *B. nursei* var. *tetrachromus* by Friese). A queen from north-western Kashmir with the pale pubescence of the thorax and tergum I yellow as well as on tergum II (Fig. 327) was described by Tkalců (1989) under the name *Pyrobombus lepidus* subsp. *hilaris*. Some individuals of both sexes from further to the east in Tibet (Wang, 1982, 1987; BMNH, PW), Yunnan (Bischoff, 1936; Wang, 1987; BMNH), Sichuan (BMNH) and Shanxi (Yasumatsu, 1951) also have all of the pale pubescence yellow. These individuals were described by Bischoff (1936) under the name *B. yuennanicola*, which Tkalců (1989) has regarded as a subspecies of *B. lepidus*. For females of *B. yuennanicola*, the many close, fine punctures of the post-ocular area of the head do not extend as far anteriorly among the large punctures of the lateral part of the ocello-ocular area, although the difference is subtle. The male genitalia have the shoulder of the penis valve particularly convex and the inner margin of the gonostylus is more deeply and broadly concave (Wang, 1982: fig. 39; PW). Both the yellow individuals and the white individuals apparently occur together at the same localities in the far east of Tibet (Wang, 1982: Jomda & Chagyab) and in Yunnan (Wang, 1987: Dongchuan). However, a male from Tibet described by Friese (1913) under the name *B. genitalis* is more extensively yellow like the males of *B. lepidus*, although the genitalia are more similar to those of *B. yuennanicola*. It is possible that these bees are all part of the same interbreeding population, in which the shape of the gonostylus and the colour of the pale pubescence show more or less correlated patterns of variation. Much more information on interbreeding and variation is needed to establish the status of the nominal taxa in this group.

DISTRIBUTION. *B. lepidus* is a peri-Tibetan species (Map 39). It is known from Shanxi (Yasumatsu, 1951), Gansu (Skorikov, 1912*b*; Bischoff, 1936; Wang, 1982; ZS), Qinghai (Skorikov, 1912*b*; Wang, 1982; BMNH, ZI), Yunnan (Bischoff, 1936; Wang, 1987; BMNH, MNHU), Tibet (Friese, 1913; Wang, 1982; BMNH, MNHU, PW), Nepal (Tkalců, 1974*b*; BMNH), Himachal Pradesh (BMNH, PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. lepidus* is recorded from the Hindu Raj range, from the southern side of the Great Himalaya range and from the Pir Panjal range, primarily from around the upper limit of the montane coniferous forest (Map 40, Fig. 6): 23 queens, 79 workers, 22 males, from 11 localities 2400–4600 m (BMNH, MNHU, NR, PW, ZS).

VARIATION WITHIN KASHMIR. Females from the Hindu Raj and Karakoram ranges have the pale pubescence of the thorax and terga I-II yellow and have very few black hairs on tergum III (Figs 327 & 328).

Queens and workers from the Kishanganga valley have a variable amount of grey-white hair intermixed on the head. The pale pubescence of the thorax and of tergum I is grey-white (tergum II remains yellow), and there are very few or no black hairs on tergum III (Figs 330 & 331). Females from Mt Apharwat are similar, although the lateral margins of tergum II are fringed with more of the white hairs (Figs 333 & 334), and one queen has all of the pubescence of tergum II cream-white.

Yellow females (Figs 327 & 328) are similar to some of the *B. himalayanus* (Figs 242 & 243) and *B. keriensis* (Fig. 404 & 407) that may occur with them. White and yellow workers of this species are particularly closely similar in colour pattern (Figs 331 & 334) to the *B. lemniscatus* (Figs 325 & 326) and *B. biroi* (Fig. 339) workers that occur with them at some localities in the Kishanganga valley and around the Vale of Kashmir. White and yellow females also resemble some of the *B. himalayanus* (Figs 247–249), *B. novus* males (Fig. 262), *B. kashmirensis* (Fig. 203) and *B. rufofasciatus* (Figs 435 & 436). *B. lepidus* can be recognised by the characters given in the key (couplets 19 & 21). The yellow males with red hairs on the apical terga may be similar in colour pattern (Figs 329 & 332) to the males of *B. pyrosoma* (Fig. 430), which occur with them at some localities. *B. lepidus* males can be recognised by their small size and by their rounded gonostyli (Figs 188 & 189).

FOOD PLANTS. (Ranunculaceae) *Aconitum laeve* Royle, *A. heterophyllum* Wallich ex Royle; (Balsaminaceae) *Impatiens glandulifera* Royle; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced].

Bombus (Pyrobombus) biroi Vogt

(Figs 42, 70, 71, 110, 111, 150, 151, 190, 191, 214, 217, 335–346, Maps 41 & 42)

Bombus (Pratobombus) biroï Vogt, 1911: 51. Lectotype queen by designation of Tkalců (1969*a*: 195), U.S.S.R.: Kirgiziya S.S.R., Alai mountains, 1905 (TM) [examined].

Bombus (Pratobombus) biroï [var.] *flavobistriatus* Vogt, 1911: 52 (see Note 1 below). LECTOTYPE queen by present designation (see Note 2 below), U.S.S.R.: Kirgiziya S.S.R., Naryn, 5.vi.1904 (ITZ) [examined]. **Syn. n.**

[*Bombus (Pratobombus) biroï flavostriatus* Vogt, 1911: 52 [examined]. Infrasubspecific (see Note 1 below) (Art. 45g(ii)(1)), unavailable name.]

[*Bombus (Pratobombus) biroï flavofasciatus* Vogt, 1911: 52 [examined]. Infrasubspecific (see Note 1 below) (Art. 45g(ii)(1)), unavailable name.]

Bombus nursei Friese, 1918: 84. Holotype queen by monotypy (see Note 3 below), INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (MNHU) [examined]. **Syn. n.**

Bombus abbotti Cockerell, 1922: 2. Holotype queen by original designation [p. 3], CHINA: Xinjiang, Taghdumbash, 13000 ft [4000 m], 11.vii.1894 (*Abbott*) (USNM) [examined]. Synonymised with *Pyrobombus biroi* (Vogt) by Tkalců (1969*a*).

Bombus agnatus Skorikov, 1933*b*: 248. Lectotype queen by designation of Podbolotskaya (in press), INDIA: Kashmir, Ladakh, Khardung La, 2–4.vii.1912 (*Jacobson*) (ZI) [examined]. Junior primary homonym of *Bombus lapponicus* var. *agnatus* Skorikov, 1912*a* [not infrasubspecific after Tkalců, 1969*a* (Art. 45g(ii)(1))]. Provisional synonym.

Bombus (Pratobombus) kotzschi Reinig, 1940: 227. Holotype male by monotypy, presumed lost (see Note 4 below), AFGHANISTAN: Baghlan, Andarab, 4000–4500 m, viii.1936 (*Kotzsch*) [not seen]. Synonymised with *Bombus agnatus* Skorikov by Tkalců, 1969*a*. Provisional synonym.

NOMENCLATURE. Note 1. Vogt states (1911:50, footnote 1) that he intends 'Varietas geographica' to be equivalent to subspecies in rank and 'Aberratio extrema' to be of infrasubspecific rank. He uses 'Forma' for taxa that he could not assign to either rank with certainty. In the second paragraph on page 52 he describes 'Die Varietät von Narynj und dem Boro-Chorogebirge . . .' and the first name used in this paragraph is '(*flavobistriatus*)'. This is deemed to be the subspecific name that was intended for individuals from this area with this colour pattern, which Vogt characterised by a greater tendency towards a yellowish colour for the pale pubescence. The four names that follow in the same paragraph are all applied to what can be regarded as variants of this local colour pattern, even though only the first two (*dyspostzonatus* and *nigrozonatus*) have their infrasubspecific status specified by the use of the term 'ab.'. Therefore the taxon named *flavobistriatus* is deemed to be of subspecific rank, whereas *flavostriatus* and *flavofasciatus* are deemed to be of infrasubspecific rank (Art. 45g(ii)(1)).

TYPE MATERIAL. Note 2. Vogt's description of *B. biroi* var. *flavobistriatus* does not specify the number of specimens examined. A single queen in the ITZ collection agrees with the original description and carries a label (1) 'Narynj / 5.6.04'; (2) a red, handwritten label 'flavobistriatus / Type'; (3) 'Collectie / C. et O. Vogt / Acq. 1960'. This specimen, which lacks only the left antenna, is designated as lectotype (Art. 74a).

Note 3. Friese's description of *B. nursei* specifies a single queen. A single queen in the MNHU collection agrees with the original description and carries labels with the data quoted, together with a red, printed label 'Type' and one of Friese's determination labels 'Bombus / nursei', dated 1909. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 4. Reinig's description of *B. kotzschi* specifies a single male from Andarab. This specimen could not be found either in the ITZ collection (W. Hogenes *in litt.*) or in the ZS collection (E. Diller *in litt.*), which are the collections with many of Reinig's bumble bee type- specimens. According to P. Rasmont (*in litt.*), any of Reinig's pre-war material not in the ITZ collection must be considered to have been destroyed by soldiers during the winter of 1945. The types of *P. rupestris* subsp. *elisabethae* Reinig, 1940, from Afghanistan in the ZS collection may have survived because they were on loan to a colleague.

AFFINITIES. Among the Old World species of the subgenus *Pyrobombus* (see the comments on *B. hypnorum*), the male genitalia of *B. biroi* are very distinctive, because the sickle-shaped, recurved hook of the penis valve head is strongly broadened and apically rounded (Figs 70 & 71; Krüger, 1943: p. 530 figs 30–45). The other species that share this character state belong to the North American *flavifrons*-group (?synapomorphy of the broad hook of the penis valve head) (the 'Flavifrons group' of Thorp, 1969). This includes at least *B. flavifrons* Cresson, *B. centralis* Cresson, *B. vandykei* (Frison), *B. caliginosus* (Frison) and *B. vagans* Smith. *B. sandersoni* Franklin and *B.*

frigidus Smith are similar but have the hook of the penis valve head less strongly broadened.

The closest relatives of *B. biroi* in the Old World may include the species of the *pratorum*-group, which are primarily Eurosiberian (see e.g. Løken, 1973; BMNH). Among the species of the subgenus *Pyrobombus*, they have relatively undifferentiated male genitalia. But for *B. jonellus* (Kirby), *B. pyrenaeus* Pérez and *B. brodmannicus* Vogt in particular, not only is the ventro-lateral angle of the penis valve just nearer to the base than to the head of the penis valve (as for species of the *flavifrons*-group and *B. biroi*, Figs 110 & 111), but the recurved hook of the penis valve head is also weakly broadened (see Krüger, 1943: 530). *B. jonellus* is widespread in the northern parts of Europe and of the U.S.S.R. (e.g. Panfilov, 1982: map 150) and reaches eastwards to western Canada (where it occurs together with *B. flavifrons*; PW). *B. pyrenaeus* is known from the mountains of southern Europe, including the Pyrenees, the Alps, the Carpathians and the Balkans (e.g. Tkalců, 1969*b*; BMNH, PW). *B. brodmannicus* is known from both the western Alps and from Turkey and the Caucasus (e.g. Tkalců, 1973; BMNH, PW). The females of *B. biroi* can be distinguished by their few, scattered, small punctures among the large punctures of the post ocello-ocular areas of the head, where the other species have these areas closely and evenly covered with small punctures.

The lectotype queen of *B. biroi* from the Alai mountains has the pale bands on the thorax and on terga I-II grey-white, whereas the pubescence of terga I-II is yellow for the queen described by Vogt (1911) under the name *B. biroi* var. *flavobistriatus*. Queens from the Himalaya are closely similar in morphology, but the grey-white pubescence is often extensively replaced by black, especially on the thorax and on tergum I (described under the name *B. nursei* by Friese, 1918).

Although the single male described under the name *B. kotzschi* is apparently no longer available (see Note 4), Reinig's description of the broader recurved hook of the penis valve head (Reinig, 1940: 228 'ist der Uncus etwas kräftige entwickelt als bei *B. pratorum*.') and of the unbanded yellow colour pattern, similar to *B. semenovianus*, agrees most closely with two males from the Zanskar mountains that are otherwise similar to *B. biroi* (Figs 70 & 71). Variation in the male genitalia of *B. biroi* is greatest in the breadth of the recurved head of the penis valve, but this is not associated with the variation in the colour pattern of the pubescence. It appears to have no more than individual significance and the males from Zanskar are within the range of variation for banded *B. biroi* (e.g. Krüger, 1943: p. 530 figs 30–45). Females with a similar, unbanded yellow colour pattern were described from Ladakh by Skorikov (1933*b*) under the name *B. agnatus*. More recently, Tkalců (1969*a*) synonymised *B. kotzschi* with *B. agnatus*, but listed them as a separate species from *Pyrobombus biroi* without further comment. From an examination of the available material, the unbanded yellow females of *B. agnatus* seem to be closely similar in morphology to the banded yellow and white females of *B. biroi* from Kashmir, as well as to the banded yellow females of *B. biroi* from further north in central Asia. There is some variation in the extent of the fine punctures in the ocello-ocular area and in the breadth of the labral lamella of the females, especially among individuals of *B. nursei*. These characters also vary considerably within each nominal taxon so that they do not appear to be diagnostic. Thus *B. biroi* and *B. kotzschi* (as the oldest available name for *B. agnatus*) may be two separate species, but until there is better evidence against interbreeding than just differences in colour pattern, I consider that they are most likely to be parts of the same species, *B. biroi*. More material is needed from the possible hybrid zone to the north of the Great Himalaya range in order to resolve the problem.

DISTRIBUTION. *B. biroi* is a central Asian species (Map 41). It is known from Mongolia (BMNH, PW), the Tien Shan (Vogt, 1911; Skorikov, 1931; Krüger, 1943; BMNH, ITZ, TM), the Pamir (Cockerell, 1922; Reinig, 1930, 1934; Skorikov, 1931; USNM), the Hindu Kush (Reinig, 1934, 1940; Tkalců, 1969*a*; BMNH), Kashmir and Himachal Pradesh (BMNH, PW).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. biroi* is recorded from the Hindu Raj, Ladakh, Zanskar, Great Himalaya and Pir Panjal ranges, in subalpine scrub (Map 42, Fig. 6): 14 queens, 38 workers, 12 males, from 13 localities 2300–4600 m (BMNH, MNHU, NR, PW, ZI).

During July 1986, I saw queens investigate gaps among the large boulders that were lying in gullies in the subalpine zone of Mt Apharwat. However, I could not find any colonies there in August or September.

VARIATION WITHIN KASHMIR. Females from the Hindu Raj range have the thoracic dorsum uniformly yellow and terga I-III black (5/5 queens, 1/1 workers, Fig. 335), like the lectotype queen of *B. agnatus* from Ladakh. A single worker from Rumbak in the Zanskar ranges has yellow hairs intermixed on tergum I (Fig. 336). Two males from the Zanskar ranges at Panichar near Suru and at Tungri (Fig. 337) have the pubescence of the thorax, of tergum I and of the basal three-quarters of tergum II uniformly yellow, with the apical and lateral margins of tergum II, all of tergum III and for the male from Suru, the basal margin of tergum IV black. This colour pattern is otherwise known for this species only from the Hindu Kush ranges (BMNH).

The species may not vary much in colour pattern on the southern side of the Great Himalaya range, where light individuals occur (Figs 338–340), but it is very variable in the Pir Panjal range, where dark individuals (Figs 341–346), similar to those from Himachal Pradesh, also occur. On Mt Apharwat the variation is chiefly in the form of (a) a reduction of the pale thoracic bands to an almost completely black thorax, with only a few pale hairs intermixed anterior to the wing bases; (b) replacement of the red with black progressively across terga III-VI, the darkest queen retaining red only on the posterior median part of tergum IV and on the anterior median part of tergum V; and (c) replacement of the yellow with white on tergum II. Reduction of the pale thoracic pubescence is pronounced for all 4 queens (Figs 341, 344, 346), but less common among workers (2/18 workers, Fig. 345). Complete replacement of yellow with white on tergum II may be common among queens (2/4 queens, Figs 341, 346) and among workers with broad bands of pale pubescence on the thorax (6/16 workers, Fig. 342).

The unbanded yellow individuals of this species (Figs 335–337) are closely similar to some *B. subtypicus* (Figs 319–324), although they have not been found together. They are also similar to some *B. avinoviellus* (Fig. 232), *B. marussinus* (Figs 254–257), *B. branickii* (Fig. 265), *B. asiaticus* (Figs 371–376) and *B. semenovianus* (Figs 397–402) that may occur with them. Unbanded yellow *B. biroi* can be recognised by the characters given in the key (couplets 19 & 20). The light, white and yellow individuals (Figs 338 & 339) are closely similar in colour pattern to the *B. lemniscatus* (Figs 325 & 326) and *B. lepidus* (Figs 330, 331, 333, 334) that occur with them at some localities. They also resemble some of the *B. himalayanus* (Figs 247–252), *B. novus* males (Figs 260 & 262), *B. kashmirensis* (Figs 302–304) and *B. rufofasciatus* (Figs 435 & 437) that occur with them. *B. biroi* can be recognised by the characters given in the key (couplets 19 & 20). The queens with a dark thorax and a white tergum II (Figs 341 & 346) resemble some of the *B. himalayanus* (Fig. 250) and *B. kashmirensis* (Figs 308 & 309) that occur in the same area. *B. biroi* can be distinguished from these by its combination of a shiny outer surface to the hind tibia and by its simple mandibles, which lack the many, pronounced teeth of *B. kashmirensis*. Some of the darkest individuals of *B. biroi* (Figs 344 & 345) show some similarity in colour pattern to some individuals of *B. haemorrhoidalis* or *B. trifasciatus* but have the oculo-malar distance much shorter. These species are completely segregated by altitude. The banded yellow males (Figs 340 & 343) are similar in colour pattern to the males of *B. keriensis* (Figs 410 & 416) that occur with them, but can be recognised by the broader recurved hooks of the head of the penis valve (Figs 70 & 71).

FOOD PLANTS. Unidentified dandelion-like composites; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Picrorhiza kurrooa* Royle ex Benth.

Subgenus ***BOMBUS*** Latreille

Leucobombus Dalla Torre, 1880: 40 (as a subgenus of *Bombus* Latreille). Type species: *Apis terrestris* Linnaeus, 1758: 578 = *Bombus terrestris* (Linnaeus), by subsequent designation of Sandhouse (1943: 564). Synonymised with *Bombus* Latreille s.str. by Milliron (1961).

Terrestribombus Vogt, 1911: 55 (as a subgenus of *Bombus* Latreille). Type species: *Apis terrestris* Linnaeus, 1758: 578 = *Bombus terrestris* (Linnaeus), by subsequent designation of Frison (1927: 67). Synonymised with *Bombus* Latreille s.str. by Skorikov (1931).

Authors have disagreed concerning the correct application of the name *Apis terrestris* Linnaeus (see the comments on *B. lucorum*). This is currently under consideration by the ICZN but does not affect the application of the name *Bombus* s.str.

For a general description of both sexes see Richards (1968).

Bombus (Bombus) tunicatus Smith

(Figs 72, 73, 112, 113, 152, 153, 192, 193, 347–355, Maps 43 & 44)

Bombus tunicatus Smith, 1852*a*: 43. Lectotype queen by designation of Tkalců (1974*b*: 325), INDIA: north, no further data (BMNH) [examined].

Bombus gilgitensis Cockerell, 1905: 223. Holotype queen by monotypy (see Note below), PAKISTAN: Gilgit (BMNH) [examined]. Change of status to *Bombus tunicatus* [Rasse] *gilgitensis* Cockerell by Tkalců (1969*a*). **Syn. n.**

Bombus terrestris var. *simlaënsis* Friese, 1909:

674. Lectotype queen by designation of Tkalců (1974*b*: 325), INDIA: Kashmir, '2–3000' [?m], vi.1904 (MNHU) [not seen]. Synonymised with *Bombus tunicatus* subsp. *tunicatus* Smith by Tkalců (1974*b*).

Bombus terrestris var. *fulvocinctus* Friese, 1909: 674. Type worker not found (Tkalců, 1974*b*), INDIA: Himachal Pradesh, Simla [not seen]. Synonymised with *Bombus tunicatus* Smith by Tkalců (1974*b*).

TYPE MATERIAL. Note. Cockerell's description of *B. gilgitensis* specifies a single queen. A single queen in the BMNH collection agrees with the original description and carries a label 'Gilgit' and another label 'Bombus / gilgitensis / Ckll TYPE', in handwriting identical to that of Cockerell. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. The species of the subgenera *Festivobombus* Tkalců, *Rufipedibombus* Skorikov, *Pressibombus* Frison and most *Bombus* s.str. share a subapical constriction of the volsella (?synapomorphy). The species of the subgenera *Rufipedibombus*, *Pressibombus* and *Bombus* share an enlargement of the outer ridge of the penis valve head and a reduction of the exterio-apical corner of the gonostylus (synapomorphies). The species of the subgenera *Pressibombus* (which includes only the east Himalayan *B. pressus* (Frison)) and *Bombus* share a ventrally and apically directed extension of the outer ridge of the penis valve head (synapomorphy). The species of the subgenus *Bombus* share a loss of the recurved hook of the penis valve head and a great broadening of the ventrally directed outer ridge, so that the penis valve heads are flared outwards to form a funnel (Figs 72–75, 112–115) (synapomorphy). The volsella shows a secondary distal broadening by the extension of its broad interio-apical process inwards towards the midline of the body (Figs 152–155) (?synapomorphy of the subgenus *Bombus*).

Within the subgenus *Bombus* there are a very large number of nominal taxa, although there is relatively little variation in morphology in comparison with some apparently monophyletic subgenera with fewer species, such as *Subterraneobombus*. The male genitalia of the Eurosiberian *B. sporadicus* Nylander (distribution mapped by Tkalců, 1967: 45) have broader and straighter penis valves in lateral aspect than do those of *B. (Pressibombus) pressus* (synapomorphy of the subgenus *Bombus*). However, for *B. sporadicus* the subapical inner margin of the penis valve is nearly straight or convex in dorsal aspect, the interio-apical corner of the gonostylus is produced beyond the exterio-apical corner by a distance along the axis of the gonocoxite that is nearly equal to the breadth of the volsella below its interio-apical process, the interio-basal process of the gonostylus is particularly weakly sclerotised and the volsella projects beyond the gonostylus in dorsal aspect by more than its own breadth below its interio-apical process (?plesiomorphies within the subgenus *Bombus*, showing some similarity to *B. pressus*). The females of *B. pressus* and *B. sporadicus* share a lack of large punctures in the posterior part of the ocello-ocular area (for *B. sporadicus* see Tkalců, 1967: fig. 1).

The male genitalia of all species of the subgenus *Bombus* except *B. sporadicus* have the subapical inner margin of the penis valve concave in dorsal aspect (usually with a small rounded projection interio-basally, particularly Figs 72 & 73), the gonostylus has the interio-apical corner produced beyond the exterio-apical corner by a distance that is much less than the breadth of the volsella (Figs 192–195), the interio-basal projection of the gonostylus is strongly sclerotised, and the exterio-apical corner of the volsella projects beyond the gonostylus in dorsal aspect usually by much less than its own breadth (synapomorphies of *B. tunicatus* + *B. franklini* + *B. affinis* + *terrestris*-group). Species of the *terrestris*-group (see the comments on *B. lucorum*) have the ventro-basal angle of the penis valve marked with a much more pronounced right angle in lateral aspect (Figs 114 & 115) (synapomorphy).

B. tunicatus is unique among the Old-World species of the subgenus *Bombus* for the combination of a reduced projection of the interio-apical corner of the gonostylus (Figs 192 & 193) and a broadly obtuse form of the ventro-basal angle of the penis valve (Figs 112 & 113). The other species with these character states, *B. franklini* (Frison) and *B. affinis* Cresson, are restricted to a small area near the west coast of North America (see Thorp *et al.*, 1983) and to the eastern side of North America (see Milliron, 1971) respectively. Males of *B. tunicatus* are unique among all species of the subgenus in that they have the gonostylus extended by the development of a distal shelf, so that the interio-apical corner is often particularly broadly curved (Figs 192 & 193). The queens can be distinguished by a distinct band of fine punctures in a slight groove at the midline of the clypeus.

Cockerell described a queen under the name *B. gilgitensis* from north-western Kashmir that differs from those from the Vale of Kashmir and from those of the eastern Himalaya by an extensive replacement of the pale pubescence by black on the scutellum and on terga I-II. These dark females from the lower Indus valley are otherwise closely similar to *B. tunicatus* s.str. and are considered to be part of the same species (see below).

DISTRIBUTION. *B. tunicatus* is a Himalayan species (Map 43). It is known from Sikkim (Bingham, 1897; Friese, 1918; Skorikov, 1933*b*), Nepal (Tkalců, 1974*b*; BMNH, NMS), Uttar Pradesh (Bingham, 1897; Frison, 1935; BMNH, MNHN, UM), Himachal Pradesh (Friese, 1909; Cockerell, 1917; Frison, 1935; BMNH, MNHN, PW), Kashmir, Pakistan (Frison, 1933, 1935; PW) and the Hindu Kush (Tkalců, 1969*a*). It may also have been genuinely recorded from the Indian plains, at Calcutta (Dover, 1922).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. tunicatus* is recorded from the Hindu Raj, Karakoram, Ladakh, Great Himalaya and Pir Panjal ranges, where it is widespread among habitats, if most abundant around the lower montane coniferous forest (Map 44, Fig. 6): 149 queens, 569 workers, 195 males, from 37 localities 1600–4100 m (AB, BMNH, BPBM, IZ, NR, PW, RH, TL, ZM, ZS).

A colony was found in woodland near Harwan (1700 m, 10.ix.1985). The nest entrance was a hole 3 cm wide in the soil amongst grass, 1m from the foot of a tree.

VARIATION WITHIN KASHMIR. Queens from the southern side of the Great Himalaya range and from the Pir Panjal range have a lighter colour pattern, with the pubescence of the scutellum, tergum I and most of tergum II grey-white (Figs 350 & 353). The workers differ in that the black band between the wing bases is more often reduced or replaced by grey-white hairs, and the pale pubescence of tergum II is usually chocolate-brown (Figs 351 & 354). Males may have tergum II either grey-white (Fig. 355) or chocolate-brown (Fig. 352).

Queens from the northern side of the Great Himalaya and from the Karakoram and Hindu Raj ranges are darker, with the pale pubescence of the scutellum and of terga I-II almost completely replaced by black (Fig. 347). The workers and males associated with these queens retain a pronounced pale band on the scutellum, but the black band between the wing bases always extends over at least one-third of the length of the thorax (Figs 348 & 349). The chocolate-brown pubescence is replaced by black on all but a narrow crescent in the middle of the base of tergum II.

Most individuals from all localities can be identified with one or other of these two extremes of the variation within Kashmir, so that there appear to be regional differences in colour pattern without much overlap. For this species of the low to mid montane zones, the segregation of the light individuals in the Jhelum valley watershed (Vale of Kashmir and the Kishanganga valley), from the dark individuals of the Indus valley watershed (Map 44), is consistent with regional colour variation as parts of a single interbreeding population and a single species. Opportunities for dispersal of individuals over the intervening barrier of high mountain ridges may perhaps have been restricted, which could have resulted in the apparently narrow colour cline (cf. the comments on *B. lucorum*).

Light queens of this species (Figs 350 & 353) are most similar in colour pattern to the *B. avinoviellus* (Figs 238–241) and *B. asiaticus* (Figs 383–389) that occur with them at some localities in the Vale of Kashmir. They also resemble some *B. kashmirensis* (Figs 305–307), *B. biroi* (Figs 341 & 342) and *B. keriensis* (Figs 408 & 409). Queens of *B. tunicatus* can be recognised by their large size, by the short oculo-malar distance and by the strongly arched posterior margin of the hind basitarsus. Workers that lack a black band on the thorax (Fig. 354) can be closely similar in colour pattern to workers of *B. simillimus* (Figs 418 & 420), but can usually be recognised easily because they have tergum I white rather than chocolate-brown, which is very rare for *B. simillimus*. Males can be recognised by their outwardly flared heads of the penis valves (Figs 72, 73, 112, 113).

FOOD PLANTS. (Ranunculaceae) *Aconitum heterophyllum* Wallich ex Royle, *A. hookeri* Stapf; (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Lupinus* sp. [introduced]; (Sambucaceae) *Lonicera quinquelocularis* Hardw.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., *Centaurea iberica* Trevir ex Spengel, unidentified yellow thistle-like composites, unidentified dandelion-like composites; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Digitalis lanata* Ehrh. [introduced], *D. purpurea* L. [introduced], *Pedicularis punctata* Decne.; (Acanthaceae) *Pteracanthus urticifolius* (Kuntze) Bremek.; (Labiateae) *Stachys sericea* Wallich ex Benth., *Prunella vulgaris* L.

Bombus (Bombus) lucorum (Linnaeus)

(Figs 74, 75, 114, 115, 154, 155, 194, 195, 356–370, Maps 45 & 46)

[*Apis terrestris* Linnaeus, 1758: 578. Lectotype queen by designation of Day (1979: 74), 'in Europa', no further data (LSL) [examined]. Application temporarily suspended (see Note 3 below) (Art. 80c).]

Apis lucorum Linnaeus, 1761: 425. Lectotype male by designation of Day (1979: 66), SWEDEN: no further data (LSL) [examined]. Synonymised with *Bombus terrestris* (Linnaeus) by Day (1979).

Apis cryptarum Fabricius, 1775: 379. Lectotype queen by designation of Løken (1966: 199), DENMARK: Copenhagen (Kiel) [not seen]. Change of status to *Bombus terrestris* var. *cryptarum* (Fabricius) by Thomson (1872); synonymised with *Bombus lucorum* (Linnaeus) by Løken (1966). Provisional synonym.

Bombus lucorum (Linnaeus); Fabricius, 1804: 350.

Bombus modestus Cresson, 1863: 99. Holotype queen by monotypy (see Note 4 below), U.S.A./CANADA: Yukon river, no further data (*Kennicott*) [not seen]. Junior primary homonym of *Bombus modestus* Eversmann, 1852. Synonymised with *Bombus lucorum* [subsp.] *lucorum* (Linnaeus) by Milliron (1971).

Bombus moderatus Cresson, 1863: 109. Replacement name for *B. modestus* Cresson. Synonymised with *Bombus lucorum* [subsp.] *lucorum* (Linnaeus) by Milliron (1971).

[*Bombus lucorum* ab. *mongolicus* Vogt, 1909: 42. Infrasubspecific (see Note 1 below) (Art. 45f(iv)), unavailable name (Art. 45e).]

Bombus (Terrestribombus) lucorum forma *magnus* Vogt, 1911: 56. Syntype queens, BRITAIN: northern Scotland; Orkney Isles (ITZ) [not seen]. Synonymised with *Bombus lucorum* (Linnaeus) by Pekkarinen (1979). Provisional synonym.

[*Bombus (Terrestribombus) lucorum mongolicus* Vogt, 1911: 56. Published without description or indication, unavailable name (Art. 12a).]

Bombus lucorum subsp. *jacobsoni* Skorikov, 1912*b*: 610. Lectotype queen by designation of Podbolotskaya (in press), INDIA: Kashmir, Maru, Fargabad, 19.v.1910 (*Trubetskoy*) (ZI) [examined]. **Syn. n.**

Bombus terrestris var. *lucocryptarum* Ball, 1914: 82. Lectotype queen by designation of Rasmont (1981: 151), BELGIUM: Brabant, Molenstede, 6.v.1913 (Brussels) [not seen]. Synonymised with *Bombus cryptarum* (Fabricius) by Rasmont (1983*a*). Provisional synonym.

Bombus pratorum var. *longipennis* Friese, 1918: 83. LECTOTYPE worker by present designation (see Note 5 below), INDIA: Sikkim, no further data (MNHU) [examined]. **Syn. n.**

Bombus (Terrestribombus) lucorum var. *alaiensis* Reinig, 1930: 107 (see Note 2 below). 3 syntype queens, 7 syntype workers, U.S.S.R.: Kirgiziya S.S.R.; Tadzhikistan S.S.R., 1950–3700 m, 21.vi–28.vii.1928 (ITZ) [not seen]. Synonymised with *Bombus lucorum* subsp. *jacobsoni* Skorikov by Tkalců (1969*a*). **Syn. n.**

[*Bombus lucorum mongolicus* Skorikov, 1933*a*: 57. Published without description or adequate indication (only Vogt, 1911, cited), unavailable name (Art. 12a).]

Bombus (Terrestribombus) magnus Rasse *mongolicus* Krüger, 1954: 276 [by indication of Vogt, 1909: 42]. LECTOTYPE queen by present designation (see Note 6 below), MONGOLIA: north, no further data, 1892 (*Leder*) (ITZ) [examined]. Change of status to *Bombus lucorum* [subsp.] *mongolicus* Krüger [cited as Vogt] by Tkalců (1974*a*). **Syn. n.**

Bombus reinigi Tkalců, 1974*b*: 322. Holotype queen by original designation, NEPAL: Ringmo to Phoksumdo lake, 3700 m, 10.vi.1973 (*Martens*) (NM) [examined]. **Syn. n.**

NOMENCLATURE. Note 1. Vogt's (1909) term 'ab.' must be taken to indicate infrasubspecific status (Art. 45f(ii, iv)). For his subsequent paper, Vogt states explicitly (1911: 50 footnote 1) that he intends 'Varietas geographica' to be equivalent to subspecies in rank and 'Aberratio extrema' to be of infrasubspecific rank. He uses 'Forma' for taxa that he could not assign to either rank with certainty and these are treated as being of subspecific rank (Art. 45g(ii)).

Note 2. Reinig's use (1930: 83 etc.) of the term 'ssp.' elsewhere in his paper is taken to indicate that infrasubspecific rank is meant for *B. lucorum* var. *alaiensis*. However, this name has subsequently been treated as a name in the species group by Krüger (1951), so it is deemed to be of subspecific rank (Art. 45g(ii)(1)).

TYPE MATERIAL. Note 3. Both Løken (1973) and Day (1979) noted that the only admissible syntype material of *A. terrestris* Linnaeus did not agree with the traditional interpretation of the taxon (which corresponds to Harris's *Apis audax*, 1776: 130, not of page 137), but instead may be a queen of the same species as *B. lucorum*. This syntype queen has since been identified as conspecific with *B. cryptarum* (Fabricius) by Rasmont (1988: 52). If this is the only admissible syntype, then the many citations of *B. terrestris* in its traditional sense must refer to misidentifications of Linnaeus's taxon. This is unfortunate because the name *B. terrestris* appears particularly widely in the literature on physiology, behaviour and ecology. To minimise any possible confusion an application has been submitted to the ICZN to use its plenary powers for the conservation of the traditional application of *B. terrestris* (Løken, Pekkarinen & Rasmont, unpublished).

Note 4. Cresson's description of *B. modestus*

(1863) specifies that a single female was examined. If found, this specimen which was originally in the 'Coll. Smith. Inst.' should be regarded as the holotype (Art. 73a(ii)).

Note 5. Friese's description of *B. pratorum* var. *longipennis* (1918) lists three queens and one worker from Sikkim. I have seen three workers from the MNHU collection that agree with the original description and carry labels with the data 'Sikkim / Coll. Bingham' and Friese's determination labels. Large workers of species of the subgenus *Bombus* are often similar in size to small queens of species of the subgenus *Pyrobombus*. One of these workers in the MNHU collection carries the labels (1) 'Sikkim / Coll. Bingham'; (2) '*B. prat.* / v. *longipennis* / [female] 1914 Friese det. / n. n.'; (3) a handwritten label 'selbstandige Art'; (4) 'LECTOTYPE / *Bombus prato- / rum* var. *longi / pennis* Tkalců det. / Friese' [designation not published, see Tkalců, 1974*b*: 324, footnote 4]; (5) 'Zool. Mus. / Berlin'. This specimen, which lacks the left hind leg, is designated as lectotype (Art. 74a).

Note 6. Krüger (1954) elevates Vogt's *B. lucorum* ab. *mongolicus* to subspecific rank as part of the nominal taxon *B. magnus*. Vogt's original description of *B. lucorum* ab. *mongolicus* refers to more than one specimen. A queen in the ITZ collection agrees with the original description and carries a label (1) '*mongolicus Vogt*' in handwriting identical to that of Vogt; (2) 'terrestris / det. Kohl.'; (3) '.gelb'; (4) a label with two illegible lines written in pencil, possibly 'B terrestris v. / or lucorum'; (5) 'N. Mongolei / Leder 92'; (6) 'Coll. Zoologisch / Museum / Amsterdam'; (7) a red printed label 'TYPE'; (8) 'LECTOTYPUS / B.lucorum ab. / mongolicus Vogt / [female] Tkalců det.' [designation not published]. This specimen, which lacks the distal joints of the right hind tarsus, is designated as lectotype (Art. 74a).

Affinities. *B. lucorum* is one of the least well understood bumble bee taxa at present and application of the name has been a matter of opinion. There is both a biological problem in determining how many species of the *terrestris*-group are present in Europe and Asia, and a nomenclatural problem (see Note 3 above) that has arisen from what appears to be the perpetuated misapplication of Linnaeus's name *Apis terrestris* (currently under consideration by the ICZN). The biological limits of the species for which, at present, *A. lucorum* is the oldest available name (Art. 80c) remain very much a question of the interpretation of indirect evidence.

Within the subgenus *Bombus*, species of the *terrestris*-group (see the comments on *B. tunicatus*) have the ventro-basal angle of the penis valve marked with a strongly pronounced right angle in lateral aspect (Figs 114 & 115) (synapomorphy). Only the most southerly species of the *terrestris*-group in the lowlands of eastern Asia, *B. ignitus* Smith (distribution mapped by Tkalců, 1962: 89; Sakagami, 1975: fig. 13), can be distinguished easily by the shape of the male genitalia. In particular, the apex of the penis valve head of *B. ignitus* is more elongated dorsally and finger-like, whereas the ventro-apical corner is rounded rather than acutely pointed. The remaining taxa within the *terrestris*-group are less strongly divergent in their morphology. Those differences in the form of the male genitalia that are known may not always be reliably discrete, particularly among samples from widely separated areas. Any cladistic interpretations of relationship based on them would be premature. In the northern part of its range *B. ignitus* overlaps with the east Asian *B. hypocrita* Pérez in northern China and Japan (distribution mapped by Tkalců, 1962: 89), and with the Siberian and Chinese *B. patagiatus* Nylander in northern China (distribution mapped by Tkalců, 1967: 52). In North America the *terrestris*-group is represented by the widespread *B. terricola* Kirby (probably conspecific with *B. occidentalis* Greene, see e.g. Milliron, 1971, for distribution records) and by the north-western *B. moderatus* Cresson (probably conspecific with *B. lucorum* s.l.).

In Britain, at least two species of the *terrestris*-group coexist over a large area: *B. terrestris* (of most authors after Linnaeus, but not of Linnaeus, see Note 3 above) and *B. lucorum*. They can be distinguished only by subtle differences in their morphology, by the length of the pubescence and by their colour patterns. For instance, British queens of *B. terrestris* of authors can be recognised by their larger size, by their shorter pubescence, which has broader, more golden-yellow bands (rather than lemon-yellow), and especially by the brownish or 'buff'- coloured pubescence of terga IV-V. Throughout the rest of the species' distribution at low altitudes in central and southern Europe, the pubescence of the apical terga is usually more nearly white, like that of *B. lucorum*. There, *B. terrestris* of authors must be identified using characters such as the number of small punctures in an antero-lateral cluster in the ocello-ocular area of the head (see Krüger, 1951; Løken, 1973; Pekkarinen, 1979; Rasmont, 1984). *B. terrestris* of authors can probably be considered conspecific with individuals of this group with other colour patterns that are known from the Canary Islands (described under the name *B. terrestris* var. *canariensis* Pérez) and Madeira (described under the name *B. maderensis* Erlandsson), because there is no reason to believe that these very similar nominal taxa would not interbreed if they were to occur together. *B. terrestris* of authors is otherwise known from Morocco (BMNH, PW), Algeria and Tunisia (Krüger, 1956; Løken, 1973; BMNH) and from across Europe, Turkey and the Caucasus (Krüger, 1954, 1956; Løken, 1973; Panfilov, 1981; BMNH) to Syria (BMNH, PW), Lebanon (BMNH) and the Elburz (Panfilov, 1981; BMNH); and from across the central U.S.S.R. to as far as the Tien Shan (Krüger, 1956; Panfilov, 1981) and Hindu Kush ranges (BMNH).

It is perhaps because of the difficulty in distinguishing continental European specimens of *B. lucorum* and *B. terrestris* of authors that a particular effort has been made to describe subtle differences among individuals of the *terrestris*-group. Even excluding *B. terrestris* of authors in all of its colour patterns (i.e. considering only *B. lucorum* in its broadest sense), at least 187 names have been published, although the majority are deemed to be of infrasubspecific rank (for a discussion of the status of the major groups of nominal taxa, see e.g. Krüger, 1951, 1954, 1956, 1958; Løken, 1973; Pekkarinen, 1979; Erlandsson, 1979; Delmas, 1981; Obrecht & Scholl, 1984; Rasmont, 1984; Rasmont *et al.*, 1986 and references therein). These samples of the *terrestris*-group from Europe show colour variation that is only relatively slight for females in comparison with many other species. Colour variation is more pronounced for males, with the frequencies of light and dark individuals differing among localities (e.g. Pekkarinen, 1979: fig. 7). This variation in the colour patterns of the males shows some correlation with variation in the compositions of their volatile marking secretions (Bergström *et al.*, 1973) and with variation in the mobilities of the enzymes phosphoglucomutase and esterase-1 under electrophoresis (e.g. Scholl & Obrecht, 1983; Pamilo *et al.*, 1984).

In northern Europe, samples of the *terrestris*-group that exclude *B. terrestris* of authors do show correlated patterns of variation in the colour of the pubescence and in the different phosphoglucomutase mobilities, although these combinations of character states are not strictly segregated between the two groups of individuals (Pekkarinen, 1979; Pamilo *et al.*, 1984). This apparent recombination of character states in some individuals could arise by interbreeding between the different parts of a population of a single species (*B. lucorum* s.l.). Furthermore, males with both light and dark colour patterns have been reared from the same nest (Løken, 1961).

In central Europe, Scholl & Obrecht (1983) found that individuals differed in the mobilities of not only phosphoglucomutase but also of esterase-1. As in northern Europe, the males in the two groups also tended to differ in the extent of the pale pubescence. Scholl & Obrecht interpreted the lack of individuals with double or hybrid enzyme bands expected from heterozygotes, and the lack of the alternative banding pattern between the two enzymes expected from recombinants, as evidence against interbreeding and concluded that two species were present. However, the expected heterozygote individuals with both phosphoglucomutase bands were also absent from the samples from northern Europe (Pamilo *et al.*, 1984), where interbreeding was believed to be occurring (Pekkarinen, 1979). In fact phenotypes with two phosphoglucomutase bands were found in samples from both the Alps and from the Pyrenees, although at least one of the bands had a lower mobility than expected for a heterozygote. Furthermore, the close association between the states of the two enzymes could possibly result from close genetic linkage. But in any case, a definitive interpretation of the differences between these electromorphs can only emerge from studies of genetic inheritance.

Scholl & Obrecht (1983: fig. 2) went on to describe differences in body shape between the queens with the two enzyme phenotypes, although there was considerable overlap in the variation. Pekkarinen (1979, see fig. 12) concluded that similar differences in shape among individuals from northern Europe showed a consistent allometric pattern as though they had all been taken from a single population. Scholl & Obrecht (1983; Obrecht & Scholl, 1984) also associated one of the two enzyme phenotypes (form A) particularly with highland samples, both from the Alps (where it was identified as the nominal taxon *B. cryptarum*) and from the Pyrenees (where it was identified as the nominal taxon *B. magnus*). However, covariation of size, shape, colour and enzyme mobilities is also known from across Europe within the single species of western honey bee, *Apis mellifera* Linnaeus (see Ruttner, 1988). I agree with Pamilo *et al.* (1984), who concluded from a comparison of their results with those of Scholl & Obrecht (1983), that a closer study of the pattern of associations between the colour characters, the enzyme mobilities and the male pheromone compositions of *B. lucorum* s.l. is still needed to solve the problem.

There is no direct evidence to say whether or not males or young queens with any one of the colour patterns of *B. lucorum* s.l. avoid those with any other colour pattern as potential mates in their natural habitats. Information on assortative mating in the field is central to the concept of the nature of species that is used for this review. Unfortunately the results of experiments on mating under laboratory conditions may not reflect the discrimination by specific-mate recognition systems under natural conditions (see the introduction on discrimination of species). De Jonghe (1982) showed this with bumble bees in cages, where males of *B. terrestris* of authors would even mate with young queens of *B. lucocryptarum* Ball, a nominal taxon that is more closely similar to *B. lucorum* s.str. Therefore under these artificial conditions neither positive nor negative results necessarily have implications for conspecific status. De Jonghe & Rasmont (1983) attempted to test the fertility (i.e. post-mating isolation) of five artificial crosses between three of the nominal taxa by laboratory experiment, using 11 queens that had survived the winter, of which 6 laid eggs, although none hatched. Control crosses were carried out within each of two nominal taxa. A total of 5 of these queens survived the winter, but only one queen laid eggs, which hatched normally. As de Jonghe & Rasmont stated in the discussion of their results, it is perhaps premature to attribute the failure to hatch of the eggs from the experimental crosses to genetic incompatibility on the basis of so few replicates. Nevertheless, more extensive experiments may confirm that such incompatibility exists.

At present it can be concluded that there is a broad set of individuals that appears to be discrete (*B. lucorum* in its broadest sense). Within this set there is variation in pubescence colour, morphology and enzyme mobilities. What is not resolved is whether the patterns of variation reveal entirely discrete subsets or, if they do, whether such patterns necessarily imply a lack of interbreeding between separate populations. Therefore, until more direct evidence against shared specific-mate recognition systems and interbreeding is available, I shall follow many previous authors and continue to treat these bees as parts of a single species, *B. lucorum* s.l. (see the comments on *B. hypnorum*). Of course this interpretation does not preclude the idea of some restriction of gene flow among some parts of the population (see Barton, 1988) of *B. lucorum* s.l., perhaps between the lowland and highland bees in particular. Thus *B. lucorum* is treated for the present as conspecific with the European taxa described under the names *Apis cryptarum* (infra-subspecific according to Løken, 1966, 1973; Tkalců, 1969*b*, 1975), *B. terrestris* var. *lucocryptarum* and *B. lucorum* f. *magnus* (conspecific according to Pekkarinen, 1979; Pekkarinen *et al.*, 1981); and conspecific with the Asian taxa described under the names *B. magnus* Rasse *mongolicus*, *B. lucorum* var. *alaiensis*, *B. lucorum* subsp. *jacobsoni*, *B. reinigi* and *B. pratorum* var. *longipennis*.

DISTRIBUTION. The present broad concept of *B. lucorum* leads to the conclusion that it is the most widespread of all bumble bee species, even though, unlike some (see Richards, 1973), it is not quite circumpolar (Map 45). It may include individuals recorded from Europe (e.g. Krüger, 1951; Løken, 1973; Alford, 1975; Rasmont, 1984; BMNH, PW), Turkey and the Caucasus (Krüger, 1951; Panfilov, 1981; Rasmont, 1984; BMNH) to the Elburz (Rasmont, 1984; BMNH); and from across the northern U.S.S.R. (Krüger, 1951; Panfilov, 1981; BMNH) to Mongolia (Morawitz, 1880; Vogt, 1909; Krüger, 1954, 1958; Tkalců, 1974*a*; Panfilov, 1981; ITZ, PW), Inner Mongolia (Reinig, 1936; Panfilov, 1981; Wang, 1982), Heilongjiang (Krüger, 1954, 1958), North Korea (Kim & Ito, 1987), Hokkaido in Japan (Tkalců, 1962; Sakagami & Ishikawa, 1969) and Kamchatka (Bischoff, 1930; Krüger, 1951; Panfilov, 1981; BMNH); and from Alaska almost to Hudson Bay (Milliron, 1971; BMNH, PW). In central Asia its distribution reaches southwards to the Tien Shan (Morawitz, 1880; Skorikov, 1931; Krüger, 1954; Panfilov, 1957, 1981), the Pamir (Reinig, 1930, 1934; Skorikov, 1931; Krüger, 1951, 1958; Panfilov, 1981), the Hindu Kush (Reinig, 1940), Pakistan (BMNH, PW), Kashmir, and eastwards to Himachal Pradesh (BMNH, PW), Uttar Pradesh (BMNH), Nepal (Tkalců, 1974*b*; BMNH, NMS), Sikkim (Friese, 1918; BMNH, MNHU), Tibet (Krüger, 1951, 1958; Panfilov, 1957; Wang, 1982, 1988; BMNH), northern Burma (BMNH), Yunnan (Wang, 1987), Sichuan (Wang, 1982; PW), Gansu (Bischoff, 1936; Krüger, 1951, 1958) and Shaanxi (BMNH). Part of this distribution is mapped by Panfilov (1981: map 96).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. lucorum* is recorded from the Hindu Raj and Karakoram ranges, and from the southern side of the Great Himalaya range and from the Pir Panjal range, in the upper montane coniferous forest and in subalpine scrub (Map 46, Fig. 6): 14 queens, 78 workers, 93 males, from 12 localities 2100–4600 m (BMNH, NR, PW, ZI).

VARIATION WITHIN KASHMIR. As in Europe there is some variation in the extent of the pale pubescence and in its hue. Some of the females from Kashmir (Figs 359, 363, 364, 368, 369) broadly resemble British *B. lucorum* in colour pattern, but have the yellow band across the anterior of the thorax extending down the sides of the thorax from a third to nearly half of the distance to the leg bases. The pubescence of the face, of the scutellum, and of tergum I is almost completely black and tergum II is often black in the apical quarter. The pale pubescence of the anterior thoracic dorsum of the queen may be lemon-yellow (similar to the holotype of *B. reinigi*) or grey-cream (lectotype of *B. lucorum* subsp. *jacobsoni* and one paralectotype queen, BMNH: both specimens show little wing wear, which is expected to be related to age and fading of yellow pubescence). The possibility that these cream-banded, dark individuals are semi-melanic *B. patagiatus* has been considered, but the punctures anterior to the lateral ocelli are more widely spaced (cf. Tkalců, 1967: fig. 2). The dark individuals are rare in the Hindu Raj and Karakoram ranges (1/4 queens, 0/26 workers, Fig. 359), but are more common further south in the Great Himalaya range (1/2 queens, 12/27 workers, Figs 363 & 364) and predominate in the Pir Panjal range (7/7 queens, 23/24 workers, Figs 368 & 369).

Other females from Kashmir (Figs 356, 357, 360, 361, 366) are lighter in colour, sometimes with pale pubescence on the face, but more generally on the scutellum, tergum I and almost all of tergum II (similar to *B. magnus* Rasse *mongolicus*, but with more pale pubescence). The possibility that these extensively pale individuals are *B. sporadicus* has been considered, but they have more of the large punctures in the ocello-ocular area of the head, especially posteriorly (cf. Tkalců, 1967: fig. 1). The pale hair of the thorax and of tergum II is always lemon-yellow, although it is susceptible to fading among older individuals. Most individuals that have been examined from the Hindu Raj and Karakoram ranges (2/4 queens, 26/26 workers, Figs 356, 357, 360) have this light colour pattern, although they are rare in the Great Himalaya range (0/2 queens, 0/27 workers, Fig. 361) and in the Pir Panjal range (0/7 queens, 1/24 workers collected, Fig. 366, – the frequency is actually much lower: during more than two months of field work on Mt Apharwat in each of two years, many more of the dark workers were seen, but no more of the light workers).

There is also variation in details of the morphology among these females, though this appears not to correlate closely with variation in colour. For instance, there is subtle variation in the shape and sculpturing of the labrum. These differences allow individual specimens to be recognised, but I found no discrete or reliable morphological differences in this character between individuals with the two extreme colour patterns. Variation in the sculpturing of the ocello-ocular areas also appears to be continuous rather than being ordered in discrete states, and there is no strict association between the states of these morphological and colour characters among individuals. Generally the light individuals have many fine punctures antero-laterally in the ocello-ocular area of the head, where they often form a cluster similar to that of *B. terrestris* of authors (Løken, 1973: fig. 12B; Rasmont, 1984: fig. 11). There are often few or none of these fine punctures for the yellow-banded dark individuals, although rather more for the cream-banded dark individuals. But then the four queens from the Hindu Raj range all have these fine punctures, even though only two of them have a light colour pattern (like most of the workers), one of them can be described as intermediate (only a very few pale hairs intermixed in the black pubescence of the scutellum and tergum I), and the other has a dark colour pattern (there are slightly fewer punctures on the two darker queens). In contrast, the single light worker from Mt Apharwat in the Pir Panjal range has none of these fine punctures, like most of the dark workers. Much of the material from the Great Himalaya range is more or less intermediate in these characters. For instance, half of the material from Lal Pani (0/1 queen, 11/21 workers) can be described as intermediate in colour pattern and has fine punctures on the head, whereas the remainder (1/1 queen, 10/21 workers) has a dark colour pattern and lacks these punctures.

Variation in the colour pattern of the males may be related to the two extreme colour patterns described from the females from Kashmir. The majority of males from the Pir Panjal range (6/9 males, Fig. 370) and some from the Great Himalaya range (38/82 males, Fig. 365) are extensively yellow. Other males from the Pir Panjal (3/9 males, Fig. 367), from the Great Himalaya (44/82 males, Fig. 362) and from the Hindu Raj and Karakoram ranges (2/2 males, Fig. 358) are darker, with a broad, black band on the thorax and another on tergum III. Thus the dark males are most frequent where the light or intermediate females predominate in the Karakoram and Great Himalaya ranges, whereas the light males are restricted to localities with the dark females in the Pir Panjal and Great Himalaya ranges. The gonostylus of these males varies considerably in its exterio-lateral length (Figs 194 & 195), but this variation appears to be continuous and uncorrelated with the colour pattern of the pubescence so that it is of only individual significance.

One interpretation is that the individuals from Kashmir with the extreme light or dark colour patterns of the pubescence could represent at least two separate species, with some variation within each (Rasmont *et al.*, 1986:678). The bees of this group from north-western Kashmir are more similar to some of those from central Asia, whereas those from south-eastern Kashmir resemble those from the eastern Himalaya. But my present interpretation of the specimens available from Kashmir is that a large proportion can be classed as intermediates between the extremes of variation (the intermediate female pattern is similar to that described under the name *B. lucorum* var. *alaiensis*) without any apparent discontinuity in this pattern of variation. For these bees of the subalpine and upper montane forest zones, the tendency for the frequencies of light and dark colour patterns to change between north- western and south-eastern Kashmir (Map 46) is consistent with regional variation among individuals from a single interbreeding population and a single species. There is perhaps relatively free movement of individuals along the mountain chains, which has resulted in extensive hybridisation and a broad colour cline (cf. comments on *B. tunicatus*). Some of the factors that may influence the variation in the male colour pattern are discussed in the section on the colour patterns of the Kashmir fauna.

Females of *B. lucorum* are distinctive in their appearance among the fauna of Kashmir. The yellow males with white hairs on the apical terga (Figs 365 & 370) may be similar in colour pattern to the males of *B. hypnorum* (Figs 313 & 316), which occur with them at some localities. *B. lucorum* males can be recognised by their larger size, by the numerous black hairs intermixed on the thorax and on terga III-IV and by their outwardly flared heads of the penis valves (Figs 74, 75, 114, 115).

FOOD PLANTS. (Leguminosae) *Trifolium repens* L.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., unidentified dandelion-like composites; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Digitalis lanata* Ehrh. [introduced], *Pedicularis punctata* Decne.; (Labiateae) *Prunella vulgaris* L.

Subgenus ***SIBIRICOBOMBUS*** Vogt

Sibiricobombus Vogt, 1911: 60 (as a subgenus of *Bombus* Latreille). Type species: *Apis sibirica* Fabricius, 1781: 478 = *Bombus sibiricus* (Fabricius), by subsequent designation of Sandhouse (1943: 599).

Obertobombus Reinig, 1930: 107 (as a subgenus of *Bombus* Latreille). Type species: *Bombus oberti* Morawitz, 1883: 238, by monotypy. Synonymised with *Sibiricobombus* Vogt by Richards (1968).

Obertibombus Reinig; Reinig, 1934: 167 (as a subgenus of *Bombus* Latreille). Unjustified emendation (Art. 33b(i, iii)).

Sibiricibombus Vogt; Skorikov, 1938*a*: 145. Unjustified emendation (Art. 33b(i, iii)).

For a general description of both sexes see Richards (1968).

Bombus (Sibiricobombus) asiaticus Morawitz

(Figs 19, 76–78, 116–118, 156–158, 196–198, 227, 371–391, Maps 47 & 48)

Bombus hortorum var. *asiatica* Morawitz *in* Fedtschenko, 1875: 4. Incorrect original spelling (Art. 32c(i)), without separate availability in this form (Art. 32c). LECTOTYPE worker by present designation (see Note 4 below), U.S.S.R.: ?Tadzhikistan S.S.R., 'Tschiburgan', 4530–8650 ft [1400–2600 m], 26.vi.1871 (ZMMU) [examined].

Bombus longiceps Smith, 1878*a*: 8. Syntype workers and male, INDIA: Kashmir, Ladakh, Dras; Kargil; Leh (*Stoliczka*) (Calcutta) [not seen]. Synonymy with *Bombus asiaticus* Morawitz suggested by Reinig (1940), confirmed here.

Bombus asiaticus Morawitz; Dalla Torre, 1896: 512. Justified emendation (Art. 33b(ii)).

Bombus Regeli Morawitz, 1880: 337. Lectotype queen by designation of Podbolotskaya (in press), CHINA: Xinjiang, Borohoro Shan, near Yining [= Gulja] (*Regel*) (ZI) [examined]. Synonymised with *Sibiricobombus asiaticus* (Morawitz) by Skorikov (1922).

[*Bombus regeli* ab. *miniatocaudatus* Vogt, 1909: 50 [footnote 1], not of Vogt, 1909: 56 [examined]. Infrasubspecific (Art. 45f(iv)), unavailable name (Art. 45e).]

Bombus (Sibiricobombus) regeli miniatocaudatus Vogt, 1911: 61 (see Note 1 below). Holotype male by monotypy (see Note 5 below), MONGOLIA: 'Septentrionalis', no further data (ITZ) [examined]. Junior secondary homonym in *Bombus* of *B. soroeensis* var. *miniatocaudatus* Vogt, 1909. Synonymy with *Bombus asiaticus* Morawitz suggested by Reinig (1940), confirmed here.

[*Bombus (Sibiricobombus) regeli* form. *fuscocaudatus* Vogt, 1911: 61 [examined]. Infrasubspecific (see Note 2 below) (Art. 45g(ii)(1)), unavailable name.]

[*Bombus (Sibiricobombus) regeli* form. *albocaudatus* Vogt, 1911: 61 [examined]. Infrasub-specific (see Note 2 below) (Art. 45g(ii)(1)), unavailable name.]

[*Bombus (Sibiricobombus) regeli* form. *tenuifasciatus* Vogt, 1911: 61 [examined]. Infrasubspecific (see Note 2 below) (Art. 45g(ii)(1)), unavailable name.]

Bombus (Sibiricobombus) miniatocaudatus race *falsificus* Richards, 1930: 652 (see Note 3 below). Holotype queen by original designation, CHINA: Xizang [= Tibet], Tingri, 14000 ft [4300 m], 4.vii.1924 (*Hingston*) (BMNH) [examined]. **Syn. n.**

Sibiricobombus flavodorsalis Skorikov, 1933*b*: 248. Syntype queens, INDIA: Kashmir, Ladakh, Suru valley (ZI) [not seen]. Junior secondary homonym in *Bombus* of *B. sonorus* subsp. *flavodorsalis* Franklin, 1913 [= *B. pensylvanicus* (Degeer), the correct original spelling of *B. pennsylvanicus* of authors]. Synonymy with *Bombus asiaticus* Morawitz suggested by Reinig (1940); synonymised with *Pyrobombus longiceps* (Smith) by Tkalců (1969*a*).

Sibiricobombus oshanini Skorikov, 1933*b*: 248. Syntype queens and male, INDIA: Kashmir, Ladakh, Nubra valley (ZI) [not seen]. Synonymy with *Bombus asiaticus* Morawitz suggested by Reinig (1940); synonymised with *Pyrobombus longiceps* (Smith) by Tkalců (1969*a*).

NOMENCLATURE. Note 1. Vogt states (1911: 50, footnote 1) that he intends 'Varietas geographica' to be equivalent to subspecies in rank and 'Aberratio extrema' to be of infrasubspecific rank. He uses 'Forma' for taxa that he could not assign to either rank with certainty. No particular status is specified for the trinomen *B. regeli miniatocaudatus*. Therefore it is deemed to be of subspecific rank (Art. 45f(i)).

Note 2. The other forms of *B. regeli* described by Vogt (1911) are all from the same series from 'Siebenstrom' and can be regarded as variants of one principal local colour pattern. These individuals were collectively referred to as 'typischen *regeli*'. Therefore they are deemed to be of infrasubspecific rank (Art. 45g(ii)(1)).

Note 3. Although Richards (1930: 634 etc.) used the term 'Subsp.' as well as 'var.' and 'race', he states that the 'race' *falsificus* is characteristic of a particular geographical area (p. 652: 'In the Himalayas a much paler form is found, for which I propose the name *falsificus*, race nov.'). This nominal taxon is therefore deemed to be of subspecific rank (Art. 45f(ii)).

TYPE MATERIAL. Note 4. Morawitz's description of *B. hortorum* var. *asiatica* lists several localities and a range of body lengths so that he must have had a series of specimens. I have seen a series of three queens, one large worker and three smaller workers from the ZMMU collection that agree with the original description (all have the pubescence of tergum II entirely yellow). The largest of these workers carries (1) a blue label '26'; (2) [Chiburgan]; (3) 'Bombus / hortorum L. / varietas asiatica.' in handwriting identical to that of Morawitz; (4) 'F. Morawitz / det. 1875.'; (5) '26.VI.1871'; (6) [Moscow / Zoological / Museum MGU]. This specimen, which bears data labels consistent with the original description (and is the only specimen to bear the full name on the third label) and is the least abraded and faded, but which lacks the tarsi of both mid legs and of the right hind leg, is designated as lectotype (Art. 74a).

Note 5. Vogt's description of *B. regeli* ab. *miniatocaudatus* is rather oblique, but is adequate to imply that it differs from *B. regeli* s.str. in that the pubescence of the apical terga is red. A single male in the ITZ collection agrees with this description (Vogt, 1909, specified that he had a single male with this colour pattern from central Asia) and carries a handwritten red label 'regeli= Gruppe / miniatocaudatus / Type'. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. A reduction of the ventro-basal angle of the penis valve is shared by a large group of the bumble bees with sickle-shaped, recurved hooks of the penis valve head (synapomorphy). In Kashmir this includes the species of the subgenera *Sibiricobombus* and *Melanobombus* (Figs 116–125). The ventro-basal angle of the penis valve is also reduced for the east Himalayan *B. (Festivobombus) festivus*, although in this case it is likely to be a convergent character state (as opposed to the interpretation in Williams, 1985). In contrast to the species of the subgenera *Sibiricobombus* and *Melanobombus*, *B. festivus* shares a reduction and ventral torsion of the interio-basal process of the gonostylus with the species of the subgenus *Pyrobombus*, and *B. festivus* also shares a subapical constriction of the volsella with species of the subgenus *Rufipedibombus* (?synapomorphies, see the comments on *B. hypnorum* and *B. tunicatus*).

Within the large group of bumble bees that have a reduced ventro-basal angle of the penis valve, the temperate steppe species of the subgenus *Cullumanobombus* (see Panfilov, 1951) share a reduced outer ridge of the penis valve head, a reduced interio-basal process of the gonostylus, a reduced interio-apical process of the volsella and an extended outer apical corner of the volsella (synapomorphies). Many of the remaining species that have a reduced ventro-basal angle of the penis valve appear to share a more pronounced narrowing of the volsella towards the apex (?synapomorphy, possibly secondarily expanded for *B. oberti* and for species of the *lapidarius*-group). These species include two species-groups.

Species of the first group share a concave distal margin of the recurved hook of the penis valve head (Figs 79–85) (?synapomorphy). This group includes the *oberti*-group of the subgenus *Sibiricobombus* and the species of the subgenus *Melanobombus*. The centre of diversity for this group is near Kashmir, with divergent species-groups in the Oriental region and in Europe and northern Asia (see the comments on *B. oberti*, *B. ladakhensis* and *B. simillimus*).

Species of the second group share a thickening of the volsella in its apical part, which is delimited by a strongly raised ridge. This ridge rises below the inner dorsal margin and curves back across the ventral surface, often forming a pronounced and coarsely-sculptured swelling or tubercle midway along the volsella (Figs 156–158) (synapomorphy). This second group includes the Mongolian *B. sibiricus* and the central Asian montane *asiaticus*-group of the subgenus *Sibiricobombus*, which reach westwards in the Caenozoic mountains to south-eastern Europe, as well as the large *fraternus*-group (in its broadest sense) from North America and the mountains of western South America (see below).

If this interpretation of these character states is accepted as the most likely estimate of relationships available at present, then one part of the subgenus *Sibiricobombus* would appear to be paraphyletic with respect to one monophyletic clade, whereas the other part would appear to be paraphyletic with respect to another monophyletic clade. Consequently the subgenus *Sibiricobombus* may be a polyphyletic assemblage, which would account for its apparent lack of exclusive synapomorphies. Yet females of the species that are currently placed in this subgenus do show some phenetic similarity because they usually have particularly many of the short, branched hairs that continue onto the outer surface of the hind basitarsus, below the postero-proximal corner (Figs 227 & 228, see the key, couplet 11). The use of the subgeneric name *Sibiricobombus* for what appears to be an artificial group with both *B. asiaticus* and *B. oberti* is continued here only for the sake of stability. I consider it undesirable to take any nomenclatural action until the males of *B. flaviventris* and *B. tanguticus* are available to clarify the relationships among the species-groups (see the comments on *B. oberti* and *B. simillimus*).

Within the group of species that have both a reduced ventro-basal angle of the penis valve and a thickened volsella, *B. sibiricus* has an expanded gonostylus (plesiomorphic among the species of *Sibiricobombus*) (see Skorikov, 1931: fig. 27; Tkalců, 1974*a*: fig. 4) and the volsella is only weakly thickened. *B. sibiricus* (of the '*sibiricus*-Gruppe' of Tkalců, 1974*a*) is known from the area around Mongolia (Skorikov, 1931: fig. 7). The eyes of the male are similar in relative size to those of the female. Apart from *B. sibiricus* and *B. oberti*, those males that are known from the other species of the subgenus *Sibiricobombus* all have very much enlarged eyes relative to those of the females.

Also within the group of species that have both a reduced ventro-basal angle of the penis valve and a thickened volsella, the species of the New World *fraternus*-group in its broadest sense share a reduction of the inner apical corner of the gonostylus and the thickened part of the volsella is usually more pronounced (?synapomorphies). These New World species are currently separated among what seems to be an unnecessarily large number of subgenera, most of which have very few species: *Fraternobombus* Skorikov, *Separatobombus* Frison, *Crotchiibombus* Franklin, *Brachycephalibombus* Williams, *Robustobombus* Skorikov and *Rubicundobombus* Skorikov; the volsella is further modified by a pronounced reduction of the exterio-apical corner for the other species of this group, all from Central America and the mountains of western South America, that are currently placed in the subgenera *Dasybombus* Labougle & Ayala (1985: fig. 5), *Funebribombus* Skorikov and *Coccineobombus* Skorikov (which includes *B. handlirschi* Friese) (?synapomorphy).

Also within the group of species that have both a reduced ventro-basal angle of the penis valve and a thickened volsella, the species of the *asiaticus*-group share a concavity of the outer margin of the middle part of the volsella, and the thickened part of the volsella is more pronounced particularly at the basal end, where it forms a rounded swelling or tubercle (Figs 156–158) (?synapomorphies). This tubercle may increase the contact area of the distal, coarsely-sculptured area of the male volsella for gripping the female sting base during copulation. This *asiaticus*-group includes the species of the '*niveatus*-Gruppe' of Tkalců (1974*a*), the species of the '*P. asiaticus*-Gruppe' of Tkalců (1969*a*, or '*longiceps*-Gruppe' of Tkalců, 1974*a*, 1974*b*) and *B. obtusus* of the '*morawitzi*-Gruppe' of Tkalců (1969*a*, 1974*a*, but not *B. morawitzi* Radoszkowski, see the comments on *B. oberti*).

Among the nominal taxa of the *asiaticus*-group, *B. obtusus* Richards from the Hindu Kush ranges has a broadly rounded gonostylus with a broad interio-basal process, and the inner margin of the head of the penis valve has only a single, straight dorsal ridge (plesiomorphic within *Sibiricobombus*). Three worker paratypes (BMNH) that are from the same locality as the holotype male (Richards, 1951) have few of the short, branched hairs arising from the outer surface of the hind basitarsus, so that this area appears to be more shining than for *B. asiaticus*, and the pubescence is generally shorter. These characteristics of *B. obtusus* remain segregated where it is known to occur with *B. asiaticus*, without any evidence of recombination in the small samples that are available.

The males of the remaining species of the *asiaticus*-group share a slight reduction of the outer apical corner of the gonostylus, and the interio-dorsal ridge at the base of the penis valve head curves from its dorsal origin to the ventral margin before it joins the recurved hook (synapomorphies of *B. asiaticus* + *B. niveatus* [+ *B. vorticosus*] + *B. sulfureus*). Males of the many nominal taxa that are similar to *B. asiaticus* share a narrowing of the volsella towards the apex from the inner margin, so that it appears even more strongly inwardly-curved (Figs 156–158) (apomorphy).

The males of *B. niveatus* Kriechbaumer, *B. vorticosus* Gerstaecker and *B. sulfureus* Friese share the ventrally-curved form of the interio-dorsal ridge at the base of the penis valve head, but also show an unusually pronounced development of an interio-ventral ridge at the base of the penis valve head (synapomorphy) (see Skorikov, 1931: fig. 29). *B. niveatus*, *B. vorticosus* and *B. sulfureus* also retain the tubercle of the volsella despite a subapical expansion of the volsella (synapomorphy) (see Skorikov, 1931: fig. 29), which is most pronounced for *B. sulfureus* (?autapomorphy). The only known differences between *B. niveatus* and *B. vorticosus* are in colour (Vogt, 1909; Pittioni, 1938). *B. niveatus* has the bands of light pubescence grey-white, whereas they are yellow for *B. vorticosus*. *B. vorticosus* is broadly distributed between Krasnovodsk and the Elburz mountains in the east to Yugoslavia in the west (e.g. Vogt, 1909, 1911; Pittioni, 1938; Reinig, 1967, 1971, 1974; Tkalců, 1969*b*; BMNH, PW). *B. niveatus* apparently occurs only within the more central part of this area, where it is less abundant (e.g. Vogt, 1909; Pittioni, 1938; Reinig, 1967, 1971, 1974; D. B. Baker, pers. comm.; BMNH, PW). Reinig (1967) described some individuals as possible hybrids and it may be that the banded white individuals and the banded yellow individuals are both parts of a single species, *B. niveatus* (cf. the comments on yellow or white *B. keriensis*). *B. sulfureus* is a rare species that occurs from the Elburz mountains to Turkey (e.g. Reinig, 1971, 1974; BMNH).

Reinig (1940) suggested that the many similar nominal taxa of the central Asian *asiaticus*-group (apart from *B. obtusus*) might actually be individuals with different colour patterns within a single species, *B. asiaticus*, but he lacked sufficient material, especially of the males, to draw firm conclusions. Individuals of the *asiaticus*-group from Ladakh have an unbanded, yellow thorax (Figs 371–376, described under the names *B. longiceps* Smith; *Sibiricobombus flavodorsalis* Skorikov; *Sibiricobombus oshanini* Skorikov). Individuals from the the other side of the Great Himalaya range in the Vale of Kashmir usually have a grey-white thorax with a black band between the wing bases (Figs 383–391, referred to as *B. callophenax* Cockerell by Richards, 1930: 652, a misidentification, see the comments on *B. avinoviellus*). There is also variation in the extent of pale pubescence on terga I-II and in the colour of the wings, which are usually more clouded with brown (infuscated) among specimens from the Vale of Kashmir. There is variation in the shape of the male genitalia, especially as to whether the gonostylus has the apical margin convex or concave and whether or not the interio-basal process is constricted near its base (Figs 196–198). However, individuals with both principal colour patterns show all forms of the gonostylus, so the variation appears to be of only individual significance.

The male mate-searching behaviour of the unbanded yellow individuals and of the banded white individuals could not be distinguished (see the introduction on male mate-searching behaviour and on the inference of allopatric, conspecific taxa). Individuals with both regional colour patterns occupy similar open habitats. The males all perch to watch for potential mates in a similar way and race in pursuit of moving objects (but without holding exclusive territories, cf. the comments on *B. rufofasciatus*). At a few localities between the two regions where individuals with each of the principal colour patterns predominate, other individuals have been collected that have colour patterns with combinations of the character states of both regional colour patterns (Figs 377–382, see the comments below on variation within Kashmir). This pattern of variation is consistent with hybridisation between individuals with divergent colour patterns within a single population (see the comments on variation below and the discussion section on the variation of *B. asiaticus* in Kashmir). Therefore these, and probably the many other nominal taxa of the central Asian *asiaticus*-group for which intermediates are known (i.e. apart from *B. obtusus*), including the banded and pale-yellow *B. miniatocaudatus* race *falsificus* from southern Tibet, are likely to be interbreeding as parts of a single species. Three further nominal taxa (*B. huangcens*, *B. heicens* and *B. xionglaris*), similar to *B. miniatocaudatus* race *falsificus*, have been described by Wang (1982) from Tibet (not seen).

DISTRIBUTION. *B. asiaticus* is a central Asian and Tibetan species (Map 47). It is known from Mongolia (Vogt, 1909; ITZ, PW), the Altai (Skorikov, 1931), the Tien Shan (Morawitz, 1875, 1880; Vogt, 1911; Skorikov, 1931; Panfilov, 1957; BMNH, ZI, ZMMU), the Pamir (Friese, 1913; Reinig, 1930, 1934; Skorikov, 1931; BMNH), the Hindu Kush (Reinig, 1940; Richards, 1951; Tkalců, 1969*a*; BMNH), Pakistan (BMNH, PW), Kashmir, Himachal Pradesh (BMNH, PW), Uttar Pradesh (BMNH), Nepal (Tkalců, 1974*b*; BMNH, NMS), Tibet (Richards, 1930; Wang, 1982; BMNH), Qinghai (Bischoff, 1936; Tkalců, 1961; Wang, 1982; BMNH, ZS) and Gansu (Bischoff, 1936).

MATERIAL EXAMINED FROM KASHMIR. *B. asiaticus* is widespread in Kashmir, recorded from the Hindu Raj, Karakoram, Ladakh, Zanskar, Great Himalaya and Pir Panjal ranges, down to the margins of the valley floor in the Vale of Kashmir. Although it is widespread among open habitats, it is most abundant in large meadows in the montane forest zone (Map 48, Fig. 6): 156 queens, 428 workers, 434 males, from 42 localities 1800–4800 m (AB, BMNH, BPBM, FA, IZ, MI, MNHN, NR, PW, RH, SEMK, TL, ZM).

Two colonies were found at Leh (3500 m, 8.vii.1980, 19.ix.1986). The nest entrances were between rocks in dry-stone walls.

VARIATION WITHIN KASHMIR. Even within Kashmir there is great variation in the colour pattern of this species (Figs 371–391, Map 48), often even within samples from a single locality. Only the principal aspects of this variation are described here.

All of the individuals from the Hindu Raj, Karakoram, Ladakh and Zanskar ranges, and from across the Great Himalaya range from the northern side to at least as far as Gumri, have the pubescence of the thorax yellow without a black band between the wing bases (Figs 371–376). These individuals from the arid region show relatively little variation, except in the replacement of black pubescence with yellow on terga I-II (Figs 374–376), which is especially pronounced for all of the specimens from central Zanskar (2 queens, 1 worker, 3 males). Individuals with this unbanded yellow colour pattern are also known from the Hindu Kush ranges, but not from Tibet, where individuals have the thoracic pubescence yellow but with a black band between the wing bases.

Most of the individuals from the Kishanganga valley (16/16 queens, 80/83 workers, 105/114 males) and from around the Vale of Kashmir (24/26 queens, 132/198 workers, 42/82 males) have an obvious band of black hairs between the wing bases (Figs 377–382, 386–391). Most of these specimens have some pale pubescence on terga I-II (Figs 377–389). Some of the individuals from the Kishanganga valley (9/16 queens, 35/83 workers, 4/114 males, Fig. 381) and almost all of those from around the Vale of Kashmir (24/26 queens, 197/198 workers, 37/82 males, Figs 383–387, 389–391) have the pale pubescence grey-white rather than yellow. Individuals from the more mesic region of the western Himalaya to at least as far east as Nepal also have the pale pubescence grey-white with a black band between the wing bases.

Individuals from a few localities in the higher valleys of the Great Himalaya range show complex variation with intermediates between the unbanded yellow colour pattern that is common in Ladakh, and the banded white colour pattern that is common in the Vale of Kashmir. This is especially evident among the material from Lal Pani in the upper Kishanganga valley (Table 7, e.g. Figs 380–382), and from Nigagar in the upper Sind valley (e.g. Figs 377–379). These two samples are also unusual because they include specimens that have the red pubescence of the apical terga largely or completely replaced by black (Lal Pani: 2/5 queens, 4/17 workers, 48/92 males, Figs 380 & 381; Nigagar: 0/2 queens, 2/12 workers, 2/6 males, Fig. 379). Individuals with this colour pattern are otherwise known only from the Hindu Kush ranges (BMNH). For an analysis of these data, see the discussion of the variation and genetics of *B. asiaticus* in Kashmir.

The individuals with an unbanded yellow thoracic dorsum (Figs 371–376) are closely similar in colour pattern to some of the *B. avinoviellus* (Fig. 232), *B. marussinus* (Figs 254–257), *B. branickii* (Fig. 265), *B. subtypicus* (Figs 319–324), *B. biroi* (Figs 335–337) and *B. semenovianus* (Figs 397–402) that occur with them at some localities. The banded white individuals of this species (Figs 381, 386, 387, 389–391) are closely similar in colour pattern to some of the *B. avinoviellus* (Figs 238–

241), *B. kashmirensis* (Figs 305–307), *B. biroi* (Fig. 342), *B. keriensis* (Figs 408 & 409) and to the queens and some males of *B. tunicatus* (Figs 350, 353, 355) that occur with them at some localities in the Vale of Kashmir. Females of *B. asiaticus* can be recognised by their very long oculo-malar distance, by the many fine punctures between the compound eye and the base of the mandible and by the many short hairs at the base of the hind basitarsus (Fig. 227, see the key, couplet 11). The males are easily recognised by their combination of greatly enlarged eyes and very long antennae.

FOOD PLANTS. **Kashmir**: (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L., *Lupinus* sp. [introduced], unidentified pink clover-like legume; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., unidentified green-flowered thistle-like composite; (Scrophulariaceae) *Digitalis lanata* Ehrh. [introduced], *D. purpurea* L. [introduced], *Pedicularis punctata* Decne.; (Labiateae) *Prunella vulgaris* L.

Ladakh: (Leguminosae) *Medicago falcata* L., *Trifolium repens* L., *Caragana versicolor* (Wallich) Benth.; (Compositae) *Echinops cornigerus* DC.; (Scrophulariaceae) *Verbascum thapsus* L.; (Labiateae) *Stachys tibetica* Vatke, *Nepeta podostachys* Benth., *Prunella vulgaris* L.

Bombus (Sibiricobombus) oberti Morawitz

(Figs 20, 79, 119, 159, 199, 228, 230, 392, 393, Maps 49 & 50)

Bombus Oberti Morawitz, 1883: 238. LECTOTYPE male by present designation (see the Note below), U.S.S.R.: Kazakhstan S.S.R., mountains near Alma Ata (*Kuschakewitsch*) (ZI) [examined].

Bombus Semenovi Morawitz, 1886: 198. Lectotype queen by designation of Podbolotskaya (in press), CHINA: Qinghai, valley of the Huang He [= Yellow River], 13500 ft [4100 m] (*Prshewalski*) (ZI) [examined]. **Syn. n.**

Bombus (Subterraneobombus) duanjiaoris Wang, 1982: 444. Holotype worker by original designation [not seen]. Paratype worker, CHINA: Xizang [= Tibet], Rutog, 5100–5400 m, 23.viii. 1976 (*Huang*) (IZ) [examined]. **Syn. n.**

TYPE MATERIAL. Note. Morawitz described *B. oberti* from males from [p. 240] 'Im Hochgebirge bei Wernoye'. At the end of this description he noted that a queen, which he also described, was most probably of the same species (p. 240: 'Als *Weibchen* gehört höchst wahrscheinlich zu vorstehend beschriebenem Männchen folgendes.'). However, because this specimen was only doubtfully included in the taxon, it cannot be considered to be a syntype. This is unfortunate, because Skorikov (1931) subsequently used the term 'Typus' in reference to a 'defekte' queen of Morawitz's *B. oberti* from 'Vernyj' [= Alma Ata, in the Tien Shan region], which might otherwise have been taken to be a valid lectotype designation (Art. 74b). Skorikov also mentions four males with the same locality labels 'Vernyj', but states that this species was never collected there again. The existence of several syntype males is indicated in the original description of *B. oberti* by the range of size measurements. I have seen a male from the ZI collection that agrees with the original description, carries a label 'Werkoye / Oberti' and lacks the right antennal flagellum, which is designated as lectotype (Art. 74a).

AFFINITIES. Within the subgenus *Sibiricobombus* (see the comments on *B. asiaticus*), *B. oberti* shares with *B. morawitzi* (see Skorikov, 1931: fig. 28) a constriction of the recurved hook of the penis valve head that is shown to a lesser extent by many species of the subgenus *Melanobombus* (Figs 79–85) (?synapomorphy of *B. morawitzi* + *B. oberti* + *Melanobombus*). But only *B. morawitzi* and *B. oberti* share the strongly curved form of this narrowed hook (Fig. 79) (?synapomorphy).

B. morawitzi (of the '*morawitzi*-Gruppe' of Tkalců, 1969*a*, 1974*a*, in part) is known from the Tien Shan (Morawitz, 1883; Skorikov, 1931; BMNH), the Pamir (Reinig, 1930, 1934; Skorikov, 1931; BMNH) and the Hindu Kush ranges (Reinig, 1940; Tkalců, 1969*a*). Unlike *B. oberti*, the males have greatly enlarged eyes relative to the females.

Another species that may be closely related has been recorded from just across the Tibetan border from Ladakh by Wang (1982: Shazia). Friese (1905) described some females from Qinghai and Gansu that have the pubescence of terga I-III yellow and of terga IV-VI black, under the name *B. flaviventris*. I have seen one of Friese's queens labelled 'Kukunor' (MNHU), but not the putative male he described later (Friese, 1909) under the same name. Richards (1930) described a series of females from southern Tibet under the name *B. (Subterraneobombus) flaviventris* subsp. *ochrobasis*. Friese's queen (MNHU) and all of Richards's material in the BMNH appears to belong to the subgenus *Sibiricobombus*, although no males are present from which to confirm this. These females have the malar area extensively punctured, the lateral ocellus is separated from the dorsal margin of the compound eye by less than two ocellar diameters, the outer surface of the hind tibia is coarsely sculptured, the many short hairs at the base of the hind basitarsus extend onto the outer surface, which has a particularly dense covering of short branched hairs, and tergum VI has a shallow apical notch and a subapical rounded boss. In all of these characters they resemble females of *B. morawitzi* most closely, but differ in that the clypeus is nearly smooth, with only a few, very widely-spaced punctures and the subapical boss of tergum VI is rounded rather than V-shaped. *B. flaviventris* has also been recorded from Tibet by Wang (1982) and from Qinghai by Skorikov (1931) and Panfilov (1957).

B. oberti is morphologically very distinct within the subgenus *Sibiricobombus*, both in the characteristics of the female (see the key) and in the form of the male volsella, which has a produced exterio-apical corner but is broadly rounded interio-apically with a very reduced interio-apical process (Fig. 159; Reinig, 1930: fig. 19; Skorikov, 1931: fig. 30). Reinig (1930) separated this species from the other species of the subgenus *Sibiricobombus* in the monobasic subgenus *Obertobombus* (the '*oberti*-Gruppe' of Tkalců, 1974*a*) (the identity of Reinig's material was discussed by Skorikov, 1931; Reinig, 1934), although this name has since been regarded as a synonym of *Sibiricobombus* (e.g. Richards, 1968; Ito, 1985). Any further nomenclatural action is considered undesirable at least until the males of *B. flaviventris* and *B. tanguticus* (see the comments on *B. simillimus*) are available to elucidate the relationships of the *oberti*-group to the species of the subgenus *Melanobombus*.

Skorikov (1931) found scarcely any difference between morphometric characters of *B. oberti* and *B. semenovi*. I can find no evidence that these nominal taxa are not parts of the same species. A worker from just across the Chinese border from Nimaling in western Tibet (IZ), which was described under the name *B. duanjiaoris* by Wang (1982), has a broad black band on tergum III like queens of *B. oberti* from Qinghai (ZI). The Tibetan worker has a shorter antennal segment 3 than for these queens, and the punctures of the malar area are weaker. In these characters, as well as in the colour pattern of the pubescence, it resembles the queens of *B. tanguticus* from southern Tibet (see the comments on *B. simillimus*), although they have the clypeus much more coarsely sculptured, the labral tubercles are strongly pointed and only narrowly separated, and the oculo-malar distance is distinctly shorter than the breadth of the mandible at its base. Otherwise *B. duanjiaoris* is closely similar to the queens of *B. oberti* from Ladakh and Qinghai in characters such as the pubescence of the hind basitarsus. Thus from the evidence available at present, *B. duanjiaoris* is most likely to be part of the same species as *B. oberti*, despite the small morphological differences, which may be related allometrically to body size. Wang (1982: 447) described another queen from western Tibet under the name *B. zhadaensis* as 'closely similar' to the type specimens of *B. duanjiaoris*, but with tergum III red (not seen). Individuals of this nominal taxon may also be conspecific with *B. oberti*.

DISTRIBUTION. *B. oberti* is a central Asian and Tibetan species (Map 49). It is known from the Tien Shan (Morawitz, 1883; Skorikov, 1931; ZI), the Pamir (Reinig, 1930, 1934; Panfilov, 1957; PW), Kashmir, Tibet (Wang, 1982; IZ) and Qinghai (Morawitz, 1886; Panfilov, 1957; ZI).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. oberti* is recorded only from the Zanskar mountains, in the high, arid alpine steppe (Map 50): 18 queens, Nimaling plain terminal moraine, 4800 m, 15–24.vii.1980 (*Williams*) (BMNH, IZ, PW).

VARIATION WITHIN KASHMIR. The queens from Nimaling generally have the black pubescence of tergum III largely replaced by orange-red, so that only a very few black hairs remain at the sides (Fig. 392). At most the black pubescence on tergum III is intermixed with the orange-red, except in a narrow, basal band (2/18 queens, Fig. 393).

This species is similar in colour pattern to the *B. himalayanus* (Figs 242 & 243), *B. kashmirensis* (Figs 295–300) and *B. ladakhensis* (Figs 394–396) that are known to occur with it. It is easily recognised by its large size and by the characters given in the key.

FOOD PLANTS. (Leguminosae) *Caragana versicolor* (Wallich) Benth.

Subgenus ***MELANOBOMBUS*** Dalla Torre

Melanobombus Dalla Torre, 1880: 40 (as a subgenus of *Bombus* Latreille). Type species: *Apis lapidaria* Linnaeus, 1758: 579 = *Bombus lapidarius* (Linnaeus), by subsequent designation of Sandhouse (1943: 569).

Lapidariobombus Vogt, 1911: 58 (as a subgenus of *Bombus* Latreille). Type species: *Apis lapidaria* Linnaeus, 1758: 579 = *Bombus lapidarius* (Linnaeus), by subsequent designation of Sandhouse (1943: 562). Synonymised with *Melanobombus* Dalla Torre by Milliron (1961).

Kozlovibombus Skorikov, 1922: 152. Type species: *Bombus kozlovi* Skorikov, 1910*b*: 413 [= *Bombus keriensis* Morawitz] in the sense of Skorikov, 1922 [based on misidentified males = *Bombus pyrosoma* Morawitz, see Reinig (1934: 169), requiring designation by the ICZN (see Note below)], by subsequent fixation of Sandhouse (1943: 561). Synonymised with *Lapidariobombus* Dalla Torre by Bischoff (1936).

Kozlowibombus Skorikov; Bischoff, 1936: 10 (as a subgenus of *Bombus* Latreille). Unjustified emendation (Art. 33b(i, iii)).

Lapidariibombus Vogt; Skorikov, 1938*a*: 145. Unjustified emendation (Art. 33b(i, iii)).

Tanguticobombus Pittioni, 1939*c*: 201 (as a subgenus of *Bombus* Latreille). Type species: *Bombus tanguticus* Morawitz, 1886: 200, by original designation. Synonymised with *Melanobombus* Dalla Torre by Richards (1968).

NOTE. Application of *Kozlovibombus* is a matter that should mandatorially be referred to the ICZN (Art. 70b). Since this name is treated here as a synonym of *Melanobombus* (a position that is not affected by either interpretation of the type species), I intend to take no action.

For a general description of both sexes see Richards (1968).

Bombus (Melanobombus) ladakhensis Richards

(Figs 80, 120, 160, 200, 394–396, Maps 51 & 52)

Bombus (Lapidariobombus) rufofasciatus var. *ladakhensis* Richards, 1928*b*: 336 (see Note 1 below). Holotype queen [not a worker] by monotypy (see Note 2 below), INDIA: Kashmir, Ladakh, Chushul, vi.1925 (*Meinertzhagen*) (BMNH) [examined].

Bombus (Lapidariobombus) rufofasciatus var. *phariensis* Richards, 1930: 642 (see Note 1 below). Holotype queen by original designation, CHINA: Xizang [= Tibet], Phari to Gyangze, 13000–15000 ft [4000–4600 m], vi. 1904 (*Walton*) (BMNH) [examined]. Change of status to *Pyrobombus ladakhensis* subsp. *phariensis* (Richards) by Tkalců (1974*b*). **Syn. n.**

Bombus variopictus Skorikov, 1933*b*: 248. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, CHINA: Qinghai, valley of the Huang He [= Yellow River], 13500 ft [4100 m] (*Prshewalski*) (ZI) [examined]. Synonymised with *Pyrobombus ladakhensis* subsp. *phariensis* (Richards) by Tkalců (1974*b*). **Syn. n.**

Bombus variopictus subsp. *bianchii* Skorikov, 1933*b*: 248. Syntype queen and worker, INDIA: Kashmir, Ladakh, Rupshu (ZI) [not seen]. Synonymised with *Pyrobombus ladakhensis* subsp. *ladakhensis* (Richards) by Tkalců (1974*b*).

Bombus (Pratobombus) reticulatus Bischoff, 1936: 7. Lectotype queen by designation of Tkalců (1974*b*: 336) [not seen]. Two paralectotype workers, CHINA: Gansu, Min Shan, 'Drakana', 3100–4000 m, 27 & 29.vii.1930 (MNHU) [examined]. Synonymised with *Pyrobombus ladakhensis* subsp. *phariensis* (Richards) by Tkalců (1974*b*). **Syn. n.**

Bombus (Lapidariobombus) rufo-fasciatus [subsp.] *ladakhensis* Richards; Tkalců, 1961: 353.

Pyrobombus (Melanobombus) ladakhensis (Richards); Tkalců, 1974*b*: 335.

NOMENCLATURE. Note 1. Richards's use (1928*b*: 333 etc.; 1930: 634 etc.) of the term 'Subsp.' in both papers is taken to indicate that infrasubspecific rank is meant for *B. rufofasciatus* var. *ladakhensis* and for *B. rufofasciatus* var. *phariensis*. However, these names have subsequently been treated as names in the species group by Tkalců (1961, 1974*b*), so Richards's taxa are therefore deemed to be of subspecific status (Art. 45g(ii)(1)).

TYPE MATERIAL. Note 2. Richards's description of *B. rufofasciatus* var. *ladakhensis* specifies that a single female was examined. A single queen in the BMNH collection agrees with the original description and carries the data quoted, together with a label 'B. *rufofasciatus*. Sm. / var. *ladakhensis* Richards / female. type' in handwriting identical to that of Richards. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

AFFINITIES. The species of the subgenus *Melanobombus* share a reduction in the outer ridge of the penis valve head (Figs 80–85) and a shortened form of the gonostylus with a reduced interio-basal process (Figs 200–205) (synapomorphies, see the comments on *B. asiaticus* and *B. oberti*). Females often have short, branched hairs below the postero-proximal corner of the hind basitarsus (e.g. Fig. 229), although these hairs are not as long, erect or numerous as for species of the subgenus *Sibiricobombus* (Figs 227 & 228, see the key, couplet 11).

Within the subgenus *Melanobombus*, the species of the *lapidarius*-group (the '*lapidarius*-Gruppe' of Tkalců, 1974*b*, 1989) share a further reduction of the interio-basal process of the gonostylus to a small, rounded knob (Figs 200–202) (?synapomorphy). In contrast, the species of the *rufofasciatus*-group share a further reduction of the apex of the gonostylus (Figs 203–205) (synapomorphy) (see the key, couplet 24).

Within the *lapidarius*-group, all of the species with the exception of *B. ladakhensis* share a much narrowed form of the penis valve shaft, in lateral aspect (Figs 120–122), and a narrower interio-apical process of the volsella (Figs 160–162) (synapomorphies). Males of *B. ladakhensis* differ from those of all other species of the subgenus *Melanobombus* by the recurved hook of the penis valve head, which is broadly fused to the shaft (Figs 80–82) (autapomorphy).

A queen of *B. ladakhensis* from Uttar Pradesh (BMNH) shares the yellow colour pattern with individuals from Kashmir and from neighbouring parts of the far west of Tibet (Wang, 1982). I have seen much more material from southern Tibet, for which the yellow of the pubescence is usually replaced by cream or grey-white (described under the name *B. rufofasciatus* var. *phariensis* Richards). This grey-white colour pattern resembles *B. rufofasciatus*. Skorikov (1933*b*) independently redescribed individuals with the yellow colour pattern under the name *B. variopictus* subsp. *bianchii* and redescribed those with the white colour pattern under the name *B. variopictus* s.str. Individuals with the white colour pattern were again redescribed shortly afterwards under the name *B. reticulatus* by Bischoff (1936). All of these females are closely similar in morphology and are considered to be parts of the same species.

DISTRIBUTION. *B. ladakhensis* is a Tibetan species (Map 51). It is known from Kashmir, Uttar Pradesh (BMNH), Nepal (Tkalců, 1974*b*; NMS), Sikkim (BMNH), Tibet (Richards, 1930; Wang, 1982; BMNH, MNHU), Qinghai (Morawitz, 1886; Skorikov, 1933*b*; Wang, 1982; ZI) and Gansu (Skorikov, 1933*b*; Bischoff, 1936; MNHU).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. ladakhensis* is recorded from the Zanskar and Ladakh ranges, in the high, arid alpine steppe (Map 52): 3 queens, 1 male, from 3 localities 3600–4800 m (BMNH, PW).

VARIATION WITHIN KASHMIR. The queen from Chushul has the pale bands of the thorax and of terga I-II yellow (Fig. 394). The hairs of tergum III are orange, whereas those of tergum IV are orange with white tips and those of tergum V are white. There are few black hairs on these terga and those that are present are mainly on the lateral parts of tergum III. The two queens from Nimaling share a similar yellow pattern, but the longer hairs of terga IV-V are pinkish brown to black basally with white tips, intermixed with many black hairs (Fig. 396). Black hairs are also more numerous for these two individuals on the apical part of tergum II and laterally on tergum III. The male has orange-red pubescence on terga III-V (Fig. 395).

This species is similar in colour pattern to some of the *B. himalayanus* (Figs 242 & 243), *B. kashmirensis* (Figs 295–300) and *B. oberti* (Figs 392 & 393) that are known to occur with it. It is easily recognised by the mixture of grey-white and black hairs, rather than orange-red hairs, on terga IV-VI.

FOOD PLANTS. (Leguminosae) *Caragana versicolor* (Wallich) Benth.; (Labiateae) *Mentha longifolia* (L.) Hudson.

Bombus (Melanobombus) semenovianus (Skorikov)

(Figs 81, 121, 161, 201, 229, 331, 397–402, Maps 53 & 54)

Lapidariobombus semenovianus Skorikov, 1914*a*: 127. Lectotype by designation of Podbolotskaya (in press) [not seen]. Paralectotype queen, INDIA: Kashmir, Ladakh, Stakmo pass, 13.vii. 1912 (*Jacobson*) (ZI) [examined].

Bombus (Lapidariobombus) lapidarius subsp. *problematicus* Bischoff, 1935: 255. Holotype worker by monotypy, INDIA: Kashmir, Ladakh, Lamayuru Gompa, 3300 m, 1.viii. 1930 (?MNHU) [not seen]. Synonymised with *Bombus semenovianus* (Skorikov) by Reinig (1940).

Bombus semenovianus (Skorikov); Reinig, 1935: 332.

AFFINITIES. Within the subgenus *Melanobombus*, *B. semenovianus* belongs to the *lapidarius*-group of species (see the comments on *B. ladakhensis*).

Within the *lapidarius*-group, *B. semenovianus* may be most closely related to *B. ladakhensis* (see the comments on *B. ladakhensis*). Both of these species have the hook of the penis valve head elongated and recurved to the shaft at an angle of less than 45° (Figs 80 & 81). All the other species of the *lapidarius*-group have the penis valve head slightly reduced in size (smallest for *B. lapidarius*) with the recurved hook forming an angle with the shaft of 45° or more (Fig. 82) (?synapomorphy). Males of *B. semenovianus* can be distinguished from males of all the other species of the *lapidarius*-group, including *B. ladakhensis*, by their enlarged eyes (relative to those of the females) and by the shape of the gonocoxite, which is nearly parallel-sided, rather than constricted, just proximal to the apex. The females of *B. semenovianus* have the ocello-ocular area more densely punctured than for the other species of the *lapidarius*-group, with a continuous, broad band of fine punctures along the eye margin.

Bischoff (1935) apparently redescribed *B. semenovianus* under the name *B. lapidarius* subsp. *problematicus* from a single worker from Ladakh.

DISTRIBUTION. *B. semenovianus* is a central Asian species (Map 53). It is known from the Hindu Kush (Reinig, 1940; Richards, 1951; Tkalců, 1969*a*; BMNH), Pakistan (Frison, 1935; BMNH, PW) and Kashmir.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. semenovianus* is recorded from the Hindu Raj, Karakoram, Ladakh, Zanskar and Great Himalaya ranges, in dry subalpine steppe and in high, subtropical semidesert (Map 54): 72 queens, 202 workers, 368 males, from 21 localities 2400–3700 m (BMNH, NR, PW, ZI, ZS).

A colony was found near Dras (3200 m, 10.viii. 1986). The nest entrance was under the edge of the corrugated iron roof of a hut.

VARIATION WITHIN KASHMIR. This species shows obvious variation only in the extent of the replacement of black by yellow in the pubescence of terga I-II (Figs 397–402). Extensive yellow on these terga is very common among males from all localities (Figs 399 & 402), but among the females it is only shown by a few queens from Gilgit (3/51 queens have an obvious yellow band on tergum I, Fig. 397).

This species is similar in colour pattern to some of the *B. avinoviellus* (Fig. 232), *B. marussinus* (Figs 254–257), *B. branickii* (Fig. 265), *B. subtypicus* (Figs 319–324), *B. biroi* (Figs 335–337) and *B. asiaticus* (Figs 371–376) that may occur with it at some localities. It can be recognised by the combination of the presence of many punctures in the ocello-ocular area of the head, the shining outer surface of the hind tibia and the lack of many short hairs at the base of the hind basitarsus (Fig. 229, see the key, couplet 11). The males can be recognised by their short antennae, by their slightly enlarged eyes and by the recurved hooks on the heads of the penis valves (Fig. 81).

FOOD PLANTS. (Leguminosae) *Melilotus officinalis* (L.) Pallas; (Compositae) *Echinops cornigerus* DC.; (Labiateae) *Stachys tibetica* Vatke, *Mentha longifolia* (L.) Hudson, *Perovskia abrotanoides* Karelin.

Bombus (Melanobombus) keriensis Morawitz

(Figs 82, 122, 162, 202, 403–416, Maps 55 & 56)

Bombus keriensis Morawitz, 1886: 199. Lectotype queen by designation of Podbolotskaya (in press), CHINA: Xinjiang, Kunlun Shan, mountains near Yutian [= Keriya], 9000 ft [2700 m] (*Prshewalski*) (ZI) [examined].

Bombus separandus Vogt, 1909: 58, 61 [footnote 1]. LECTOTYPE queen by present designation (see Note 3 below), CHINA: Xinjiang, Borohoro Shan (ITZ) [examined]. Change of status to *Bombus keriensis* f.g. *separandus* Vogt by Reinig (1935). **Syn. n.**

Bombus kohli Vogt, 1909: 41, 61 [footnote 2]. Syntype worker (see Note 4 below), MONGOLIA: north, no further data, 1892 (*Leder*) (ITZ) [examined]. Junior primary homonym of *Bombus kohli* Cockerell, 1906 [= *B. morio* (Swederus)]. **Syn. n.**

Bombus kohli var. *postzonatus* Vogt, 1909: 61 [footnote 2]. LECTOTYPE queen by present designation (see Note 5 below), MONGOLIA: north, no further data, 1892 (*Leder*) (ITZ) [examined]. **Syn. n.**

Bombus kozlovi Skorikov, 1910*b*: 413. Replacement name for *B. kohli* Vogt. Change of status to *Bombus keriensis* f.g. *kozlovi* Skorikov by Reinig (1935). **Syn. n.**

Bombus (Lapidariobombus) separandus incertoïdes Vogt, 1911: 58 [by indication of Vogt, 1909: 61 (footnote 1)] (see Note 1 below). Holotype queen by monotypy (see Note 6 below), MONGOLIA: north, no further data, 1892 (*Leder*) (ITZ) [examined]. **Syn. n.**

Bombus lapidarius var. *tenellus* Friese, 1913: 86. 2 syntype females and 1 syntype male, U.S.S.R.: ?Zapadnyy Sayan, 'Arasagun-gol' (*Staudinger*) (MNHU) [not seen]. Synonymised with *Lapidariobombus incertoides* (Vogt) by Skorikov (1931). **Syn. n.**

Lapidariobombus separandus subsp. *meridialis* Skorikov, 1914*a*: 127. Holotype queen by monotypy (see Note 7 below), INDIA: Kashmir, Sind valley above Sonamarg, 2400–3000 m, 9–10.vi.1912 (*Jacobson*) (ZI) [not seen]. **Syn. n.**

Bombus (Lapidariobombus) tenellus var. *alpivagus* Richards, 1930: 639 (see Note 2 below). Holotype queen by original designation, CHINA: Xinjiang, Taghdumbash, 14000 ft [4300 m], 18.vi.1913 (*Hingston*) (BMNH) [examined]. **Syn. n.**

Bombus (Lapidariobombus) kozlowi Skorikov; Bischoff, 1936: 9. Unjustified emendation (Art. 33b(i, iii)).

Pyrobombus (Melanobombus) keriensis subsp. *karakorumensis* Tkalců, 1989: 57. Holotype queen by original designation, PAKISTAN: Gilgit, Banidas 36°11′N 74°33′E, 2600 m, 30.vi–2.vii.1959 (*Lobbichler*) (ZS) [examined]. **Syn. n.**

NOMENCLATURE. Note 1. Vogt's (1911: 58) use of the name *incertoides* under 'Meine *Separandus*-tiere ...', for a female that he had described previously (1909: 61 [footnote 1]), is deemed to be of subspecific rank even though he did not state its rank explicitly (Art. 45f(i)). Skorikov subsequently (1922) treated *incertoides* as an available name and adopted it as the name of a species (Art. 45g(ii)(1)).

Note 2. Richards's use (1930: 634) of the term 'Subsp.' elsewhere in his paper could be taken to indicate that infrasubspecific rank is meant for *B. tenellus* var. *alpivagus* (despite the comment 'probably a geographical race'). However, this has subsequently been treated as a name in the species group by Reinig (1935: 333 [footnote 1: 'f.g. means forma geographica (=subsp.)']), so Richards's taxon is deemed to be of subspecific status (Art. 45f(ii)).

TYPE MATERIAL. Note 3. Vogt's original description of *B. separandus* mentions at least one female and one male from the Alai Mountains and from 'Siebenstromgebiet'. Vogt subsequently (1911: 58) refers to the same material 'aus der Umgebung des Festungswerks Narynj und dem Boro-Chorogebirge [= Borohoro Shan] im Siebenstromgebiet'. A single queen in the ITZ collection agrees with the original description and carries a label (1) 'Boro-Chorogeb / Tisilikau'; (2) a white, handwritten label 'separandus O.V.'; (3) a red printed label 'Type'. This specimen is designated as lectotype (Art. 74a).

Note 4. Vogt's description of *B. kohli* mentions two queens (one of *B. kohli* var. *postzonatus*) and a number of workers. However, the description is specified to have been made primarily from a queen that had the pubescence of tergum III black. I have seen a single worker from the ITZ collection that agrees with this description and carries a label 'N. Mongolei / Leder 92', and a red printed label 'Type'. I believe that this is one of the workers referred to at the end of footnote 2 and regard it as a syntype. It would be preferable to designate as lectotype the queen on which Vogt concentrated for the original description, when this queen is found.

Note 5. Vogt described *B. kohli* var. *postzonatus* as like the type, the queen of *B. kohli* s.str., so he probably based his description on the second of the two queens that he mentions at the end of footnote 2, rather than on any of the workers. A single queen in the ITZ collection agrees with the original description and carries a label (1) 'N. Mongolei / Leder 92'; (2) a white, handwritten label 'kohli, ab postzonatus'; (3) a white handwritten label '13'; (4) a red printed label 'Type'. This specimen is designated as lectotype (Art. 74a).

Note 6. Vogt's description of *B. separandus incertoides* specifies that only one specimen (referring to a second queen described separately under the name *B. separandus* in 1909: 61 [footnote 1]) was available. A single queen in the ITZ collection agrees with the original description and carries a white, handwritten label 'separandus- / incertoides-' and a red, printed label 'Type'. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 7. Skorikov's description of *Lapidariobombus separandus* subsp. *meridialis* specifies that only a single queen was available. If a single queen with the appropriate data can be found then this should be regarded as the holotype (Art. 73a(ii)).

AFFINITIES. Within the subgenus *Melanobombus*, *B. keriensis* belongs to the *lapidarius*-group of species (see the comments on *B. ladakhensis*).

Within the *lapidarius*-group, *B. keriensis* shares with *B. incertus* Morawitz, *B. lapidarius* (Linnaeus) and *B. sichelii* Radoszkowski a slight reduction of the recurved head of the penis valve (Fig. 82) (?synapomorphy, see comments on *B. semenovianus*). All of these species, except *B. incertus*, have the volsella narrowed near its mid point in ventral aspect (Fig. 162) (synapomorphy of *B. lapidarius* + *B. keriensis* + *B. sichelii*). *B. incertus* and *B. lapidarius* apparently do not occur east of the Caspian Sea (distributions summarised by Reinig, 1935: chart 3, 1939: fig. 15), except for a couple of records of *B. lapidarius* from the northern U.S.S.R. (Panfilov, 1981: map 92).

The closest relative of *B. keriensis* is probably *B. sichelii* Radoszkowski [the correct original spelling of *B. sicheli* of authors]. Unlike *B. lapidarius*, females of these two species share an apical notch on tergum VI and the males appear to share a slight displacement of the weak ventro-basal angle of the penis valve nearer to the mid-point of the shaft (Fig. 122). *B. sichelii* has a broad Eurosiberian distribution, although this is fragmented in Europe among the southern mountains (mapped in Reinig, 1935: charts 2 & 5, 1939: fig. 4). The distributions of the two species overlap in the Altai (Reinig, 1935; BMNH), Mongolia (Reinig, 1935; Tkalců, 1974*a*; BMNH, PW) and Gansu (Bischoff, 1936). Unlike *B. sichelii*, the males of *B. keriensis* have the apex of the penis valve head slightly less acutely pointed (Fig. 82) and the interio-apical process of the volsella is narrower, with a less prominent interio-basal corner (Fig. 162). There is considerable variation in the sculpturing of the ocello-ocular area of the females, but females of *B. keriensis* often differ from those of *B. sichelii* in that the band of fine punctures is more distinctly interrupted, so that there is a narrow shining area with only large punctures adjacent to the eye margin.

Skorikov (1931) and Reinig (1935) both suggested that the cream individuals that were described under the name *B. separandus* Vogt, which often also have pale hairs on the face and a pale fringe in the pubescence of tergum III (='ciliated', e.g. *B. kohli* var. *postzonatus* Vogt and *Lapidariobombus separandus* subsp. *meridialis* Skorikov), are actually conspecific with the more distinctly yellow and often unciliated *B. keriensis* (also described under the names *B. kohli* Vogt, *B. lapidarius* var. *tenellus* Friese, *B. tenellus* var. *alpivagus* Richards and *Pyrobombus keriensis* subsp. *karakorumensis* Tkalců). Reinig (1935) also included the unciliated and white queen described under the name *B. separandus incertoides* Vogt in this group. Individuals with the very pale and ciliated colour patterns occur throughout much of the total distribution of this group of nominal taxa, but are most frequent in the region of the Pamir (Reinig, 1935: chart 4, 1939: fig. 23). The inference that they are all likely to be interbreeding as parts of a single population and a single species is supported by the apparently continuous variation between the two extreme colour patterns among the material from the Hindu Raj range (BMNH).

A nest from the Pamir was described by Bischoff (1931).

DISTRIBUTION. *B. keriensis* is a widespread, but primarily central Asian and Tibetan species (Map 55). It is known from Mongolia (Vogt, 1909, 1911; Tkalců, 1974*a*; BMNH, ITZ, PW), the Altai (Morawitz, 1880; Friese, 1913; Skorikov, 1931), the Tien Shan (Morawitz, 1880; Vogt, 1909, 1911; Skorikov, 1931; Panfilov, 1957; BMNH, ITZ, TM), the Pamir (Richards, 1930; Reinig, 1930, 1934, 1935; Bischoff, 1931; Skorikov, 1931; BMNH), the Hindu Kush (Reinig, 1940; Richards, 1951; Tkalců, 1969*a*; BMNH), Pakistan (BMNH, PW), Kashmir, Xinjiang [Kunlun Shan] (Morawitz, 1886; TM, ZI), Tibet (Richards, 1930; Wang, 1982; BMNH), Qinghai (Morawitz, 1886; Panfilov, 1957; Tkalců, 1961; Wang, 1982; ZS) and Gansu (Bischoff, 1936). In the west it is also known from the Elburz (Skorikov, 1931; BMNH), Turkey and the Caucasus (Reinig, 1935; BMNH). Reinig (1935: chart 2, 1939: figs 4 & 23) mapped a summary of this distribution. A similar disjunct distribution between the Hindu Kush ranges on the one hand and the Elburz and Armenian highlands on the other is shown by *B. melanurus*.

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. keriensis* is recorded from the Hindu Raj, Zanskar, Great Himalaya and Pir Panjal ranges, in alpine scrub and steppe (Map 56, Fig. 6): 73 queens, 155 workers, 38 males, from 18 localities 2600–5100 m (BMNH, FA, NR, PW, ZS).

VARIATION WITHIN KASHMIR. When these bees are seen in flight, the two most obvious characters of the colour pattern to vary are (a) the yellow or white colour of the pale pubescence on the thorax and on terga I-II; and (b) the presence or absence of a fringe of pale hairs at the posterior and lateral margins of tergum III (present in the 'ciliated' state).

Females from the Hindu Raj range generally have the pale pubescence nearly white if queens, but yellow if workers, although both are strongly ciliated (cream-white: 49/50 queens, 0/68 workers, no males available; strongly ciliated: 47/50 queens, 43/68 workers; Figs 403–407). In the Great Himalaya range, workers are usually paler but unciliated, both around the Kishanganga valley (cream-white: 2/7 queens, 39/49 workers, 0/33 males; strongly ciliated: 0/7 queens, 0/49 workers, 0/33 males; Figs 408–410), and at the head of the Sind valley (cream-white: no queens available, 32/33 workers, 0/3 males; strongly ciliated: 0/32 workers, 1/3 males).

Individuals from the Zanskar ranges usually have the pale pubescence yellow and are unciliated (cream-white: 1/5 queens, 1/2 workers, no males available; strongly ciliated: 1/5 queens, 0/2 workers [more yellow and unciliated queens were seen but not collected]; Figs 411–413) like those from Tibet. Individuals from the Pir Panjal range are similar, but with slightly more extensive black pubescence on the thorax (cream-white: 0/8 queens, 0/5 workers, 0/2 males; strongly ciliated: 0/8 queens, 1/5 workers, 0/2 males; Figs 414–416).

This species is similar in colour pattern to some of the *B. himalayanus* (Fig. 242), *B. kashmirensis* (Figs 298–300, 305–307), *B. subtypicus* (Figs 317 & 318), *B. biroi* (Figs 340, 342, 343), *B. tunicatus* queens (Fig. 350), *B. asiaticus* (Figs 386–388) and *B. oberti* (Fig. 393) that occur with it at some localities. Females can usually be recognised by their combination of an apical notch on tergum VI with a lack of many short hairs at the base of the hind basitarsus (see the key, couplet 11). The males are closely similar in colour pattern (Figs 410 & 416) to some of those of *B. subtypicus* (Fig. 318) and of *B. biroi* (Figs 340 & 343), which may occur with them at some localities, but can be recognised by the narrow recurved hooks of the head of the penis valve (Fig. 82).

FOOD PLANTS. **Kashmir**: (Ranunculaceae) *Aconitum hookeri* Stapf; (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Picrorhiza kurrooa* Royle ex Benth.

Ladakh: (Leguminosae) *Caragana versicolor* (Wallich) Benth.; (Labiateae) *Stachys tibetica* Vatke.

Bombus (Melanobombus) simillimus Smith

(Plate 1, Figs 83, 123, 163, 203, 226, 417–421, Maps 57 & 58)

Bombus simillimis Smith, 1852*b*: 48. LECTOTYPE queen by present designation (see Note 3 below), INDIA: north, no further data (BMNH) [examined]. Incorrect original spelling (see Note 1 below) (Art. 32c(i)), without separate availability in this form (Art. 32d).

[*Bombus similis* Smith; Smith, 1854: 403. Incorrect subsequent spelling, unavailable name (Art. 33c). Junior primary homonym of *Bombus similis* Fabricius, 1804 [= *Centris similis* (F.)].]

Bombus simillimus Smith; Dalla Torre, 1896: 548. Justified emendation (see Note 2 below) (Art. 33b(ii)).

[*Bombus tonsus* Skorikov, 1922: 160. Published without description or indication, unavailable name (Art. 12a).]

[*Bombus tonsus* Skorikov, 1931: 202. Published without description or indication, unavailable name (Art. 12a).]

Bombus terrestris var. *grossiventris* Friese, 1931: 303. LECTOTYPE worker by present designation (see Note 4 below), INDIA: Kashmir, Srinagar, Shalimar, 1800 m, 7.x.1923 (*Fletcher*) (MNHU) [examined]. **Syn. n.**

Bremus (Sibiricobombus) oculatus Frison, 1933: 335. Holotype male by original designation [p. 338], INDIA: Himachal Pradesh, Baghi, 8800 ft [2700 m], 7–8.x.1921 (*Kemp*) (Calcutta) [not seen]. **Syn. n.**

Sibiricobombus tonsus Skorikov, 1933*b*: 248. LECTOTYPE queen by present designation (see Note 5 below), INDIA: Kashmir, Kishtwar, Datgash, 12.vi.1910 (*Trubetskoy*) (ZI) [examined]. **Syn. n.**

Bombus (Lapidariobombus) oculatus var. *haemorrhous* Richards, 1934: 87. Holotype worker by original designation [p. 88], INDIA: Himachal Pradesh, Dalhousie, 7.vii.1906 (*Barrow*) (BMNH) [examined]. **Syn. n.**

NOMENCLATURE. Note 1. Smith's original spelling (1852*b*) is '*simillimis*', which may have been intended as the superlative of *similis* (comment after the original description: 'This species is very like the *Lapidarius* of Linn.;'). There is no evidence that this spelling is incorrect from the original publication, except (Art. 32c(i)) in its termination (Art. 31b). Therefore the subsequent spelling by Smith (1854), which is not an emendation (Art. 33b), is deemed to be incorrect (Art. 33c), although the termination of *simillimis* must still be corrected (Art. 32d(ii)) to *simillimus*.

Note 2. Dalla Torre's change in the subsequent spelling of '*simillimis*' can be accepted as intentional (Art. 33b(i)), even though he only quotes '*simillimus*', because of his introduction (1896: v): 'So ist es z.B. wissenschaftlich gewiss nicht gerechtfertigt, wenn jeder Elementarlateiner befähigt und – berechtigt ist, Wörter, wie laevis, coelestis, sylvaticus zu corrigiren, ohne dass man in wissenschaftlichen Kreisen je davon Notiz genommen hat, und ähnlich verhält es sich auch mit den Geschlechtsendungen, wo auch alle erdenklichen grammatikalischen Fehler gemacht und fortwährend colportirt werden.'

TYPE MATERIAL. Note 3. Smith's description of *B. simillimus* is of a queen. A queen in the BMNH collection agrees with the original description and bears a purple-edged label (1) 'Lecto- / type'; (2) 'N. / India', reverse side '48 / 132' (this accession number refers to 73 Hymenoptera from the Boyes collection received in 1848); (3) '*N. China* / Baily 11 / 7 / 55'; (4) '60–15 / E.I.C.' (see Note 2 on *B. haemorrhoidalis*); (5) 'similis / Type Sm.'; (6) 'Bombus / *similis* / Smith Trans. / Ent. Soc. 1852'; (7) a red-edged label 'Type'; (8) 'B.M. TYPE / HYM. / 17B.981'. Other Smith syntypes might have existed and may since have become dispersed to other collections. Therefore this queen, which lacks both fore tarsi, the left front basitarsus and both hind tarsi, is designated as lectotype (Art. 74a).

Note 4. Friese described *B. terrestris* var. *grossiventris* from three workers. I have seen one of these from the MNHU collection that agrees with the original description and carries a label (1) 'Kashmir 200ft / Shalimar / Srinagar / 7 Oct. 1923 / Fletcher coll'; (2) a handwritten label 'Bombus / grossiventris / Fr. / [worker] Friese det. 25'; (3) a printed label 'Zool.Mus. / Berlin'. This specimen, which lacks the distal joints of the left hind tarsus, most of the flagellum of the right antenna and the distal joints of the left antenna, is designated as lectotype (Art. 74a).

Note 5. Skorikov's description of *Sibiricobombus tonsus* is of a queen. A queen in the ZI collection from near the village of Datgash, with a label 'B. tonsus type', agrees with the original description. Because other Skorikov syntypes may exist, this specimen, which has two lateral patches of orange-brown pubescence on the anterior part of the scutum, is designated as lectotype (Art. 74a).

AFFINITIES. Within the subgenus *Melanobombus* (see the comments on *B. ladakhensis*), *B. simillimus* belongs to a group of species, the *rufofasciatus*-group (the '*flavothoracicus*-Gruppe' + '*rufofasciatus*-Gruppe' of Tkalců, 1974*b*), for which the male gonostylus is shortened with distinct inner and outer apical corners (Figs 203–205) (synapomorphy). Skorikov (1922) recognised a subgenus *Kozlovibombus* on the basis of the male genitalia of what was probably a specimen of *B. pyrosoma* s.str. (see Reinig, 1934, 1935). Females of all of the species in this group apparently vary in colour with size (see the comments on *B. pyrosoma)* in a manner resembling that described for the Central American *B. (Pyrobombus) ephippiatus* Say by Owen & Plowright (1980) and for the Himalayan *B. (Festivobombus) festivus* by Ito *et al.* (1984). This variation is not only in the extent of the pattern of replacement of black by pale hairs in the pubescence, but smaller individuals often have at least one additional colour. This is usually yellow or brown in the pubescence on tergum II. Hence queens, workers and males may appear strikingly different (see Plate 1).

Within the *rufofasciatus*-group, queens of *B. simillimus* share with those of *B. tanguticus* Morawitz a distinct and complete sulcus obliquus of the mandible. They also share the fine, branched hairs on the outer surface of the hind tibia (Fig. 226) and the dense (often black) short pubescence on the hind basitarsus. *B. tanguticus* is known from Sikkim and Tibet (Richards, 1930; BMNH) and Qinghai (Morawitz, 1886). It could also be present in the high mountain ranges of north-eastern Kashmir (unconfirmed record from Kashmir by Skorikov, 1933*b*). Queens of *B. tanguticus* are very easily distinguished from those of *B. simillimus* by their acutely and deeply notched tergum VI, which is straight or only shallowly indented for *B. simillimus*; by their labral furrow, which is only one-quarter of the total breadth of the labrum, as opposed to nearly half of the breadth for *B. simillimus*; by their oculo-malar distance, which is about equal to the breadth of the mandible at the base, whereas it is much longer for *B. simillimus*; by their ocello-ocular area, which is much less densely punctured; by their clypeus, which is less strongly swollen, but more coarsely punctured; and by their nearly clear (subhyaline) wings. *B. tanguticus* was considered sufficiently distinctive by Pittioni (1939*c*) to warrant the description of a monobasic subgenus, *Tanguticobombus*. The male remains undescribed and apparently unknown, so that the precise relationships of this species are difficult to resolve at present.

Within the *rufofasciatus*-group, some females have a straight or only shallowly indented apex to tergum VI as well as a distinct sulcus obliquus of the mandible. Queens and workers with these characters from the western Himalaya were described under the names *B. simillimus* and *B. terrestris* var. *grossiventris* respectively. They have not been associated as castes of the same species because of their very different colour patterns. Queens of *B. terrestris* var. *grossiventris* and workers and males of *B. simillimus* were unknown. But within the *rufofasciatus*-group from the Himalaya, only these nominal taxa share the uniformly red pubescence of terga IV-V and the intensively darkened (infuscated) wings. One of the older queens (BMNH) has the pubescence of terga I-II distinctly lighter than on tergum III, so that it is dark brown rather than black (although the brown is still not as light as for *B. terrestris* var. *grossiventris*). The queens have particularly many of the fine, short, branched hairs on the outer (corbicular) surface of the hind tibia (Fig. 226), although these hairs are also present for some of the workers. These hairs are seldom numerous in this position among bumble bees, except for species of the subgenus *Psithyrus*. Among the social species, the presence of these hairs may be associated with particularly large body size because they are otherwise very numerous for *B. (Melanobombus) tanguticus* Morawitz, *B. (Rufipedibombus) rufipes* Lepeletier and *B. (Rufipedibombus) eximius* Smith, although they are also present for some queens of the European *B. lapidarius*. Almost certain confirmation that *B. simillimus* (queens, Fig. 417), *B. terrestris* var. *grossiventris* (workers, Fig. 418) and males (Fig. 419) described under the name *Bremus oculatus* by Frison (1933) are the castes and sexes of a single species comes from a colony discovered near Harwan, in the Vale of Kashmir (see Plate 1 and the description of material examined from Kashmir). The alternative interpretation is that a colony of one species, for which the queen must be unknown, had been usurped by a queen of another species, which is closely similar in morphology to the workers of the first queen.

Males of *B. simillimus* can be distinguished from those of the other taxa of the *rufofasciatus*-group by their greatly enlarged eyes; by the large, sub-rectangular gonostylus, which is scarcely reduced and retains a narrow interio-basal process (Fig. 203) (plesiomorphic within the *rufofasciatus*-

group); and by the twisted interio-apical process of the volsella (Fig. 163). The form of the gonostylus is most similar to that of *B. richardsiellus* (Tkalců, 1968*a*: figs 84–86; see the comments on *B. pyrosoma*).

A queen with two light patches on the anterior dorsum of the thorax was described under the name *Sibiricobombus tonsus* by Skorikov (1933*b*). Two workers were redescribed under the name *B. oculatus* var. *haemorrhous* by Richards (1934). These individuals are closely similar in morphology to those described under the names *B. simillimus* and *B. terrestris* var. *grossiventris* respectively and are considered to be part of the same species. Females (probably workers) of another nominal taxon from Tibet (*B. trilineatus*), which is closely similar to *B. simillimus*, have been described by Wang (1982) from slight differences in colour pattern (not seen).

DISTRIBUTION. *B. simillimus* is a west Himalayan species (Map 57). It is known only from Himachal Pradesh (Frison, 1933; Richards, 1934; BMNH), Kashmir and Pakistan (BMNH).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. simillimus* is recorded from the lower slopes in the Kishanganga valley, in the Vale of Kashmir and along tributaries to the Chenab valley, in open scrub around the lower montane coniferous forest (Map 58): 9 queens, 102 workers, 8 males, from 9 localities 1600–3000 m (AB, BMNH, MNHU, IZ, NR, PW, ZI).

I found a colony near the edge of open woodland near Harwan (1700 m, 10.ix.1985). A fresh hole, 50 cm deep by 30 cm wide, in the bank of an irrigation channel contained 6 queens (including an old and very abraded individual), 39 workers and 5 males. Returning workers found their way into the cavity via a separate tunnel, nearly 2 m long. The remains of only 4 cocoons were present in the cavity. I had seen bears (probably *Solenarctos thibetanus* (Cuvier)) in the vicinity earlier on the same day.

VARIATION WITHIN KASHMIR. There is little variation among the queens (Plate 1 and Fig. 417). The number of black hairs on the thoracic dorsum of workers does vary, but none of them has even a weak black band between the wing bases (Plate 1 and Fig. 418). One large worker (severely abraded) from the colony near Harwan has the hairs of tergum I white with dark bases, while tergum II is very dark brown, with a posterior fringe of white hairs (Fig. 420). The males vary from having terga I-II entirely nearly white (5/5 males, Harwan, Plate 1 and Fig. 419), to having tergum I white and tergum II chocolate-brown, with the exception of a posterior fringe of white hairs (3/3 males, Banihal, Fig. 421).

Queens of this species are distinctive in their appearance. Workers are similar in colour pattern to some of those of *B. tunicatus* (Figs 351 & 354), which occur with them. Workers of *B. simillimus* can usually be recognised by their chocolate-brown pubescence of tergum I (Fig. 418), rather than white as for *B. tunicatus* (Fig. 354). Males are also similar in colour pattern to some of those of *B. tunicatus* (Figs 352 & 355), or even some *B. asiaticus* (Fig. 385) that occur with them. They can be distinguished from *B. tunicatus* by their enlarged eyes and from *B. asiaticus* by their short antennae.

FOOD PLANTS. (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) unidentified pink clover-like legume; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., *Centaurea iberica* Trevir ex Spengel, unidentified yellow thistle-like composite; (Gentianaceae) *Swertia petiolata* D. Don.

Bombus (Melanobombus) pyrosoma Morawitz

(Plate 1, Figs 84, 124, 164, 204, 422–430, Maps 59 & 60)

Bombus pyrosoma Morawitz, 1890: 349. Lectotype queen by designation of Podbolotskaya (in press), CHINA: 'Gansu', 'Utai', 8900 ft [2700 m], vi.1884 (*Potanin*) (ZI) [examined].

Bombus pyrrhosoma Morawitz; Dalla Torre, 1896: 544. Unjustified emendation (Art. 33b(i, iii)).

Bombus flavothoracicus Bingham, 1897: 552. Lectotype queen by designation of Tkalců (1974*b*: 338), INDIA: Sikkim, Lintu, 12500 ft [3800 m], v.1894 (*Bingham*) (BMNH) [examined]. Junior secondary homonym in *Bombus* of *Psithyrus campestris* var. *flavothoracicus* Hoffer, 1889 [= *B. campestris* (Panzer)]. Provisional synonym.

Bombus miniatus Bingham, 1897: 553. Holotype male by original designation, INDIA: Sikkim, Lintu, 12500 ft [3800 m], v[!].1894 (*Bingham*) (BMNH) [examined]. Synonymised with *Pyrobombus flavothoracicus* (Bingham) by Tkalců (1974*b*). Provisional synonym.

[*Bombus pyrrhosoma* var. *canosocollaris* Skorikov, 1912*b*: 608 [not seen]. Infrasubspecific (Art. 45g(ii)(1)), unavailable name (Art. 45e).]

Bombus friseanus Skorikov, 1933*a*: 62. Holotype queen by monotypy (see Note 1 below), CHINA: Sichuan, Songpan, above 9500 ft

[2900 m], 1894 (*Beresovski*) (ZI) [examined]. **Syn. n.**

Bremus (Lapidariobombus) formosellus Frison, 1934: 163. Holotype male by original designation [p. 166], TAIWAN: 'Roeichi', 15.ix.1924 (*Shiraki & Sonan*) (INHS) [examined]. Provisional synonym.

Bombus (Lapidariobombus) pyrrhosoma subsp. *hönei* Bischoff, 1936: 10. LECTOTYPE queen by present designation (see Note 2 below), CHINA: Yunnan, Lijiang, 23.v.1934 (*Höne*) (MNHU) [examined]. **Syn. n.**

[*Bombus (Lapidariobombus) pyrrhosoma* f. *flavocorbicularis* Tkalců, 1961: 353 [not seen]. Infrasubspecific (Art. 45g(ii)(1)), unavailable name (Art. 45e).]

Pyrobombus (Lapidariobombus) wutaishanensis Tkalců, 1968*a*: 39. Holotype queen by original designation [p. 41], CHINA: Shanxi, Wutai Shan, 3200 m, 15.vii.1936 (*Höne*) (MNHU) [examined]. **Syn. n.**

TYPE MATERIAL. Note 1. Skorikov's description of *B. friseanus* specifies that only a single queen was examined. A single queen in the ZI collection agrees with the original description and bears a label with the data quoted. I believe that this is the single specimen on which the original description is based and regard it as the holotype (Art. 73a(ii)).

Note 2. Bischoff's description of *B. pyrrhosoma* subsp. *hoenei* shows that several females, collected '20.4' and '1.5.–23.6.34', were examined. A queen in the MNHU collection bears the label (1) 'Li-kiang. (China). / Provins Nord-Yuennan. / 23.5 1934.H.Höne.'; (2) 'pyrrhosoma / hoenei n. sp. / [female] / det. Bischoff'; (3) a red printed label 'Typus'; (4) 'LECTOTYPE / Bombus / pyrrhosoma / Tkalců det. / hönei Bischoff / [female]' [designation not published]; (5) 'Zool. Mus. / Berlin'. This specimen, which is complete, is designated as lectotype (Art. 74a).

AFFINITIES. Within the subgenus *Melanobombus* (see the comments on *B. ladakhensis*), *B. pyrosoma* belongs to the *rufofasciatus*-group of species (see the comments on *B. simillimus*).

Within the *rufofasciatus*-group, the known males, other than those of *B. simillimus*, are characterised by pronounced reductions (shortening) of the gonostylus and a broadening of its interio-basal process (Figs 204 & 205) (synapomorphies). Apart from *B. simillimus* and *B. rufofasciatus* (see the comments on *B. rufofasciatus*), four principal nominal taxa have been recognised in this group. These were described under the names *Lapidariobombus richardsiellus*, *B. pyrosoma*, *B. friseanus* and *B. flavothoracicus*. Of these, *B. pyrosoma*, *B. friseanus* and *B. flavothoracicus* are morphologically closely similar and differ from each other primarily in colour pattern.

B. richardsiellus was described (Tkalců, 1968*a*; BMNH) from 2 queens, 3 workers and 1 male from northern Burma and from the neighbouring parts of Tibet. The queens are similar to the *B. friseanus* from the same region, but have the clypeus slightly more coarsely punctured. Their white-banded colour pattern has a much more restricted distribution of pale pubescence. The 'allotype' male has the exterio-apical corner of the gonostylus more strongly reduced than for *B. simillimus* (synapomorphy of *B. richardsiellus* + *B. pyrosoma* [+ *B. friseanus*] + *B. rufofasciatus*), so that it is intermediate in form between the gonostyli of *B. simillimus* and of *B. friseanus*. Another 4 males from near the Burmese border of Tibet (BMNH) may belong to *B. richardsiellus*, but show a broad range of forms of the gonostylus, from similar to that of the 'allotype', to more like that of *B. friseanus*.

At a few localities in Kashmir (e.g. Mt Apharwat [1986], Daksum), *B. simillimus* and *B. rufofasciatus* not only occasionally occur together, but also with another taxon of the *rufofasciatus*-group. Males of *B. simillimus* and *B. rufofasciatus* have colour patterns similar to their respective workers, although the males have much larger eyes. The males of the third taxon are often predominantly yellow (Figs 424, 427, 430), unlike the females (even when reared from the same maternal colony, see Plate 1 and the comments on the material examined from Kashmir), and have eyes that are not enlarged relative to those of the females. These yellow males differ in their mate-searching behaviour from males of *B. rufofasciatus* and presumably from those of *B. simillimus* (see the introduction on male mate-searching behaviour, and the comments on *B. rufofasciatus*). There are no specimens with intermediate colour patterns or morphology as evidence that they interbreed with either *B. rufofasciatus* or *B. simillimus*. Therefore the three taxa are believed to represent three separate species.

B. flavothoracicus is the name that has been used most recently for the third Himalayan taxon of the *rufofasciatus*-group that is found in Kashmir (e.g. Tkalců, 1974*b*). This name was used by Bingham for a queen, which has light olive-yellow pubescence at the front and rear of the thorax and on tergum I. Gastral terga IV-VI have the pubescence extensively white. The predominantly yellow males were also described by Bingham, but under the name *B. miniatus*. The workers differ from the queens in that they have most of tergum II dull olive-yellow or brown and most of the pubescence of terga III-V red, which replaces most of the white and even some of the black hairs. This caste dimorphism may be size-dependent, because the red pubescence is less extensive in large workers (decreasing with increasing body size in Figs 426, 428, 429) and red may occasionally be intermixed on terga III-IV of small queens. This nominal taxon is known from as far east in the Himalaya as the area of the Sikkim/Tibet/Bhutan border (BMNH), to as far west as Kashmir. Queens of two further nominal taxa from Tibet (*B. eurythorax* and *B. stenothorax*), both very similar to *B. flavothoracicus*, have been described by Wang (1982) from slight differences in colour pattern (not seen).

Material from further to the east in Yunnan and Sichuan was described under the names *B. pyrrhosoma* subsp. *hoenei* by Bischoff (1936) and *B. friseanus* Skorikov (1933*a*) respectively. Both the queens and the workers from this region are similar in colour pattern to the workers of *B. flavothoracicus* from the Himalaya, although the pale pubescence (including tergum II) is usually a deeper orange-yellow and there are fewer black hairs intermixed with it on the thorax. Thus both castes have the pubescence of terga III-VI red, although without any distinctly white hairs. Workers of *B. friseanus* are known to occur as far west as the lower Zangbo [= Tsangpo] valley of Tibet and the Char Chu valley at the extreme eastern end of the Himalaya, adjacent to Arunachal Pradesh (BMNH, no queens available).

Material from further to the north in Gansu was originally described under the name *B. pyrosoma* s.str. by Morawitz (1890). The queens have the thorax and tergum I black with just a very few grey-white hairs intermixed. The pubescence of gastral terga II-VI is predominantly red. Morawitz also described the workers from Gansu (listed as Var. b and Var. c), which have the pubescence of the thoracic dorsum grey-white with a black band between the wing bases, with tergum I grey-white, tergum II brown and terga III-VI red. Similar material is known from the hills that reach eastwards to as far as Beijing and Hebei. Tkalců (1968*a*) described two queens under the name *Pyrobombus wutaishanensis* that have distinctly fewer fine punctures in the ocello-ocular area than *B. pyrosoma* s.str. At least one of these queens is from Shanxi. I have seen another queen of *B. pyrosoma* s.str. from neighbouring Beijing (PW) that also shows some reduction in the number and extent of these fine punctures, so that it is intermediate in this character between *Pyrobombus wutaishanensis* and, for example, *B. friseanus*. These specimens are otherwise similar in morphology and in colour pattern to the lectotype of *B. pyrosoma*. Until more evidence to the contrary is available, I consider that they are most likely to be part of the same species.

From the available material, each of the three principal colour patterns is relatively constant among the individuals of each caste from across extensive regions, with transitions in colour pattern apparently occurring over short distances. Yet from Qinghai, between the regions occupied by *B. friseanus* and *B. pyrosoma* s.str., Tkalců (1961) described a worker (*B. pyrrhosoma* f. *flavocorbicularis*, infrasubspecific under Art. 45g(i)) that has both the yellow hairs on the head and legs, as for *B. friseanus*, and the pale pubescence of the dorsum grey-white (not seen), as for workers of *B. pyrosoma* s.str. Skorikov (1912*b*) even described banded grey queens from the area of Gansu and Inner Mongolia, similar in colour pattern to most of the workers rather than to the queens with a predominantly black thoracic dorsum from north-eastern China, under the name *B. pyrrhosoma* var. *canosocollaris* (not seen). I consider it likely that these intermediate colour patterns are evidence of clines from hybrid zones between the more widespread regional colour patterns (see the comments on *B. trifasciatus*). This has also been recognised previously for the Chinese nominal taxa by Bischoff (1936) and Tkalců (1961).

Evidence of intermediates between *B. flavothoracicus* and *B. friseanus* is not as strong, at least partly because so little material is available from where these nominal taxa occur in close proximity in the eastern Himalaya. However, the few workers and males that are available from the far east of the Himalaya (BMNH) are difficult to assign to either nominal taxon with any confidence. The only available queens are two specimens from between Gyangtse [=Gyangzê] and Phari [=Pagri] in Tibet (BMNH). These large individuals share the white-'tailed' colour pattern of the west Himalayan *B. flavothoracicus* queens, although they also have red hair extensively intermixed in the pubescence of terga III-IV.

Overall, from west to east there may be a trend towards an extension of the red pubescence on the gaster, especially for queens, in which it completely replaces the white hair. There is also a parallel decrease in the extent of the pale pubescence on the thorax and on terga I-II, which is accompanied by a change in colour from light yellow to orange-yellow to grey-white.

The males that are associated with the three principal nominal taxa, *B. flavothoracicus*, *B. friseanus* and *B. pyrosoma* s.str., all have closely similar genitalia, but vary in the form of the interio-apical corner of the gonostylus. This is narrowly bilobed or spinose (similar to some putative *B. richardsiellus*) for *B. miniatus* (the male associated with *B. flavothoracicus*, Fig. 204) and also for some *B. pyrosoma* s.str., but may be broadly bilobed (similar to *B. rufofasciatus*, Fig. 205) for other *B. pyrosoma* s.str. All of these males have the pubescence predominantly yellow and their eyes are not enlarged relative to those of the females. Both of these states are characteristic of males that patrol circuits of scent-marked sites in the upper montane forest habitats to find mates (see the introduction on male mate-searching behaviour and the discussion of the colour patterns of the Kashmir fauna). Therefore from the evidence available at present I consider it likely that the three principal nominal taxa are based on the regional colour patterns of the females from a single interbreeding population. If this is the case, they would be considered to be parts of a single species. More definite conclusions concerning the status of these nominal taxa must await more direct information on their mate-searching behaviour and on interbreeding between them, particularly from the eastern Himalaya.

The name *Bremus formosellus* was applied by Frison (1934) to a population that is isolated from other *B. pyrosoma* s.l. by sea on the island of Taiwan. He distinguished this nominal taxon from *B. miniatus* by colour pattern alone, although he had apparently not seen any specimens from the Himalaya (p. 166: 'It ['This new species'] differs from the male (type) and workers of *miniatus* as described by RICHARDS (1930) in the more broader and distinct black band on the thorax between the wings and lack of bright yellow pubescence on first and second dorsal tergites.'). The grey females and the extensively yellow males of *Bremus formosellus* actually resemble closely some of the *B. pyrosoma* s.str. from Qinghai and Gansu in both colour pattern and morphology. I know of no evidence to suggest that individuals from the disjunct population on Taiwan would not interbreed with those from the continental population if they were to occur together, although I have not yet had the opportunity to examine any queens. So *Bremus formosellus* may also be a part of the species *B. pyrosoma* s.l.

DISTRIBUTION. *B. pyrosoma* is primarily a peri-Tibetan species, although it also occurs in other highland areas in northern and southern China (Map 59). It is known from Inner Mongolia (Skorikov, 1912*b*, 1933*a*; Tkalců, 1960), Hebei (Yasumatsu, 1951; PW), Beijing (PW), Shanxi (Yasumatsu, 1951; Tkalců, 1968*a*; MNHU), Shaanxi (BMNH), Hubei (Sakagami, 1972), Gansu (Morawitz, 1890; Skorikov, 1912*b*; Bischoff, 1936; ZI), Qinghai (Skorikov, 1912*b*; Panfilov, 1957; Tkalců, 1961), Sichuan (Skorikov, 1933*a*; Sakagami, 1972; Wang, 1982; BMNH, PW, ZI), Yunnan (Bischoff, 1936; Wang, 1987; BMNH, MNHU), Taiwan (Frison, 1934; Chiu, 1948; INHS, PW), Tibet (Richards, 1930; Wang, 1982, 1988; BMNH, PW), Sikkim (Bingham, 1897; Friese, 1918; Richards, 1930; BMNH, UM), Nepal (Tkalců, 1974*b*; BMNH, NMS, PW), Uttar Pradesh (Frison, 1935), Himachal Pradesh (BMNH, PW) and Kashmir. A record from Guangdong [Leizhou peninsula] (Sakagami, 1972) needs to be confirmed with more material. A similar disjunct distribution between the mountains of south-western China and Taiwan is known for *B. parthenius* (synonym of *B. sonani* (Frison), see the comments on *B. lepidus*) (Wang, 1982).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. pyrosoma* is recorded from the southern side of the Great Himalaya range and from the Pir Panjal range, in montane coniferous forest (Map 60, Fig. 6): 56 queens, 172 workers, 62 males, from 10 localities 1900–4000 m (AB, BMNH, IZ, MNHN, NR, PW, RH).

A colony was found on Mt Apharwat, in the forest below Gulmarg (2500 m, 2.ix.1985). The entrance tunnel was in the bank of a stream and lead 40 cm to the nest cavity, 80 cm vertically below the surface of the bank. The nest contained 478 small cocoons (33 occupied, 7 that were opened all contained males), 126 large cocoons (106 occupied), 20 queens, including one old and very abraded individual, 36 workers and 31 males. No younger brood was present.

VARIATION WITHIN KASHMIR. This species is very variable in colour pattern, but among the females from Kashmir the trends in variation appear to be associated more with body size than with locality (e.g. increasing body size in Figs 426, 428, 429, 425). In particular, small queens show the partial replacement of black or white pubescence by red on terga III-IV, so that they appear similar to the largest workers (Fig. 429). Most workers have, in addition, yellow (Fig. 426) to chocolate-brown (Figs 428 & 429) hair basally on tergum II, so that black hair remains only apically on tergum II and basally on tergum III (Plate 1). Some of the smallest workers have most of terga I-II dull olive-yellow and most of terga III-V orange-red (Fig. 426).

The male colour pattern is predominantly yellow (Plate 1 and Figs 424, 427, 430). The pubescence of terga III-VII varies from entirely yellow (Figs 424 & 427) to largely black on tergum III and orange-red on terga IV-VII (Fig. 430). The most frequent pattern is for the pubescence of tergum III to be yellow with a band of orange-red hairs and black hairs intermixed basally, whereas terga IV-VII are orange-red with a few black hairs laterally and a few yellow hairs apically and laterally. Only one male (from Daksum) has a well-defined black band between the wing bases.

The only pronounced geographical variation is that queens from Kel, in the Kishanganga valley, have unusually extensive patches of yellow hair on the basal half of tergum II (10/10 queens, Fig. 422). Workers from Kel (26 workers) have few black hairs on terga II-III, irrespective of size (Fig. 423). Another queen with the same data is severely abraded, so this series may represent the members of a single colony that had been collected by the Schmid cxpedition. There are also very few black hairs on the gasters of workers from 4 other sites in the Kishanganga valley (5/5 medium-sized workers, no queens available).

Queens and workers of this species are distinctive in their appearance. The yellow males with red hairs on the apical terga may be similar in colour pattern to the males of *B. lepidus* (Figs 329 & 332), which occur with them at some localities. Males of *B. pyrosoma* can be recognised by their larger size and by the short gonostylus with an interio-apical spine (Fig. 204).

FOOD PLANTS. (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L., *Lupinus* sp. [introduced]; (Sambucaceae) *Lonicera quinquelocularis* Hardw.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., unidentified dandelion-like composite; (Ericaceae) *Rhododendron anthopogon* D. Don; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced], *D. purpurea* L. [introduced], *Pedicularis rhinanthoides* Schrenk, *P. punctata* Decne.; (Labiateae) *Prunella vulgaris* L.

Bombus (Melanobombus) rufofasciatus **Smith**

(Plate 1, Figs 26, 30, 34, 38, 85, 125, 165, 205, 431–439, Maps 61 & 62)

Bombus rufo-fasciatus Smith, 1852*b*: 48. Lectotype queen by designation of Tkalců (1974*b*: 340), INDIA: north, no further data (BMNH) [examined].

Bombus Prshewalskyi Morawitz, 1880: 342. Syntype worker [not a queen] and male, CHINA: 'Gansu', no further data (*Prshewalski*) (ZI) [not seen]. Synonymised with *Bombus rufofasciatus* var. *championi* Richards by Richards (1930); synonymised with *Pyrobombus rufofasciatus* (Smith) by Tkalců (1974*b*).

Bombus rufocinctus Morawitz, 1880: 343. Lectotype queen by designation of Podbolotskaya (in press), CHINA: 'Gansu' hills, viii.1871 (*Prshewalski*) (ZI) [examined]. Junior primary homonym of *Bombus rufocinctus* Cresson, 1863. Synonymised with *Bombus rufofasciatus* Smith by Handlirsch (1888).

Bombus chinensis Dalla Torre, 1890[June 25]: 139. Replacement name for *B. rufocinctus* Morawitz. Junior secondary homonym in *Bombus* of *Apathus rupestris* var. *chinensis* Morawitz, 1890 [April 30] [= *B. chinensis* (Morawitz)]. Synonymised with *Bombus rufofasciatus* Smith by Richards (1930).

Bombus rufofasciatus var. *championi* Richards, 1928*a*: 107. Holotype queen by original designation, INDIA: Kashmir, 8000–9000 ft [2400–2700 m], vi.1901 (*Nurse*) (BMNH) [examined]. **Syn. n.**

[*Bombus (Lapidariobombus) rufofasciatus* var. *rufior* Richards, 1928*b*: 335 [examined]. Infrasubspecific (Art. 45g(ii)(1)), unavailable name (Art. 45e).]

[*Bombus (Lapidariobombus) rufofasciatus* var. *intermedius* Richards, 1930: 643 [examined]. Infrasubspecific (Art. 45g(ii)(1)), unavailable name (Art. 45e).]

Bombus (Lapidariobombus) waterstoni Richards, 1934: 88. Holotypc queen by original designation [p. 89], 'Himalayas', no further data (BMNH) [examined]. Synonymised with *Pyrobombus rufofasciatus* (Smith) by Tkalců (1974*b*).

AFFINITIES. Within the subgenus *Melanobombus* (see the comments on *B. ladakhensis*), *B. rufofasciatus* belongs to the *rufofasciatus*-group (see the comments on *B. simillimus*).

Within the *rufofasciatus*-group, *B. rufofasciatus* can be distinguished from *B. simillimus* by its strongly reduced male gonostylus (Fig. 205; see the key, couplet 25). *B. rufofasciatus* is similar to some *B. pyrosoma* s.l. in that it has a broadly bidentate, interio-apical corner of the gonostylus, although the apex of the interio-basal process usually forms a right angle rather than being distinctly acute (see the comments on *B. pyrosoma*). The females of *B. rufofasciatus* can be distinguished by their nearly clear (hyaline) wings, which are more strongly darkened (infuscated) for the other taxa of the *rufofasciatus*-group, and by their weaker punctures in the ocello-ocular area of the head. The males can be distinguished from males of *B. richardsiellus* or *B. pyrosoma* by the size and shape of their eyes, which are moderately enlarged relative to those of the females (i.e. similar in shape to those of *B. simillimus*).

The enlargement of the eyes of male *B. rufofasciatus* in comparison with the females reflects differences in their mate-searching behaviour that may contribute to a failure to interbreed with individuals of the other species where individuals of *B. rufofasciatus* occur with them (see the introduction on male mate-searching behaviour). For instance, *B. rufofasciatus* and *B. pyrosoma* overlap extensively in their foraging areas around the upper limit of the montane coniferous forest on Mt Apharwat (Fig. 6). However, workers and queens of *B. pyrosoma* are very much in the minority on the subalpine slopes above the forest, whereas those of *B. rufofasciatus* are rare within the forest. The males of *B. pyrosoma*, with eyes similar in size to those of the females, patrol circuits of scent-marked sites only within the upper montane forest. The males of *B. rufofasciatus*, with enlarged eyes, watch for potential mates from perches on open, subalpine hilltops, where they usually establish exclusive territories. So individuals from these two populations are searching for mates in different ways and in different kinds of habitat (cf. the comments on *B. asiaticus*). No intermediates could be found in samples containing both *B. rufofasciatus* and *B. pyrosoma* s.l. [= *B. flavothoracicus*] from Kashmir or Nepal (BMNH, PW); *B. rufofasciatus* and *B. richardsiellus* from northern Burma (BMNH); *B. rufofasciatus* and *B. pyrosoma* s.l. [= *B. friseanus*] from Yunnan (BMNH) or Sichuan (PW); and *B. rufofasciatus* and *B. pyrosoma* s.str. from Gansu (Bischoff, 1936).

A queen from Kashmir that has a broad band of yellow pubescence on tergum II was described under the name *B. rufofasciatus* var. *championi* by Richards (1928*a*). This individual is closely similar in morphology to those queens of *B. rufofasciatus* that have tergum II entirely black and it is considered to be part of the same species.

DISTRIBUTION. *B. rufofasciatus* is a peri-Tibetan species (Map 61). It is known from Gansu (Morawitz, 1880; Bischoff, 1936; ZI, ZS), Qinghai (Morawitz, 1886; Tkalců, 1961; Wang, 1982; PW, ZS), Tibet (Friese, 1918; Richards, 1928*a*, 1928*b*, 1930; Wang, 1982, 1988; BMNH), Sichuan (Morawitz, 1890; Wang, 1982; PW), Yunnan and northern Burma (BMNH), Arunachal Pradesh (Friese, 1918), Sikkim (Bingham, 1897; Friese, 1918; BMNH, UM), Nepal (Tkalců, 1974*b*; BMNH, NMS, PW), Uttar Pradesh (Richards, 1928*a*, 1930; BMNH), Himachal Pradesh (BMNH, PW) and Kashmir. A record from Inner Mongolia [Ordos] (Morawitz, 1880) is dubious and needs to be confirmed (cf. Skorikov, 1912*b*, on *B. pyrosoma*).

MATERIAL EXAMINED FROM KASHMIR. In Kashmir, *B. rufofasciatus* is recorded from the Hindu Raj, Great Himalaya and Pir Panjal ranges, in mesic alpine scrub (Map 62, Fig. 6): 58 queens, 351 workers, 260 males, from 28 localities 1900–4600 m (AB, BMNH, BPBM, MI, MNHN, NM, NR, PW, RH, SEMK, TL; 3 males photographed in the upper Wangat valley, 1 worker photographed in the Sangisfaid valley, C. A. Chadwell).

A colony was found on Mt Apharwat, at the lower edge of the subalpine pasture at Khilanmarg (3000 m, 4.ix.1985). The nest entrance was among boulders, mostly larger than 1 m across, that were lying several deep in a gully. This nest could not be excavated. I saw many queens investigate similar sites in the subalpine zone during July 1986, presumably in search of suitable nest sites.

VARIATION WITHIN KASHMIR. Most queens from Mt Apharwat in the Pir Panjal range have a few yellow hairs intermixed with the black near the base of tergum II (Plate 1), but some individuals (10/32 queens from Apharwat, also 2/2 queens from around the Kishanganga valley) have an obvious band of yellow pubescence on the basal half of this tergum (Fig. 434). Queens from the Hindu Raj range (12/12 queens), at the western limit of the species' distribution, are unusual in that the pubescence of tergum II is predominantly yellow, with at most only a narrow band of black hairs apically (Fig. 431). Workers and males from all parts of Kashmir generally have little black pubescence on tergum II (Plate 1 and Figs 432, 433, 435, 436, 438, 439), especially among individuals from the Hindu Raj range (Figs 432 & 433). At the opposite extreme, some of the largest workers from Apharwat have only a narrow yellow band on tergum II (Fig. 438), or even just a few yellow hairs at the base of the tergum, so that it appears generally black (2/92 workers). Queens from further to the east in the Great Himalaya range generally share the darker colour pattern (Fig. 437), whereas workers generally retain yellow pubescence on tergum II (Figs 435 & 438). A male from Batakush has the pale bands on the thorax and tergum I yellow (1/5 males).

The queens without obvious yellow pubescence on tergum II are quite distinctive in their appearance (Fig. 437). The yellow and white individuals of both castes and both sexes (Figs 431–436, 438, 439) can be particularly closely similar in colour pattern to the *B. kashmirensis* (Figs 302–304) that occur with them at some localities. *B. rufofasciatus* can be recognised by the hairs of terga III-VI, which are shorter and either red (most of terga

III-IV in workers and males; only tergum III in queens) or white (most of terga IV-VI in queens, terga V-VI in workers, terga V-VII in males), rather than red with white tips. They also resemble some of the *B. himalayanus* (Figs 247–249), *B. novus* males (Figs 260 & 262), *B. lemniscatus* (Figs 325 & 326), *B. lepidus* (Figs 330, 331, 333, 334) and *B. biroi* (Figs 338 & 339) that occur with them. Females of *B. rufofasciatus* can be recognised easily because they have terga V-VI with white hairs rather than with orange-red hairs.

FOOD PLANTS. (Ranunculaceae) *Aconitum laeve* Royle, *A. heterophyllum* Wallich ex Royle, *A. violaceum* Jacquem. ex Stapf; (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L., *Lupinus* sp. [introduced]; (Sambucaceae) *Lonicera quinquelocularis* Hardw.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., *Lactuca lessertiana* (DC.) C. B. Clarke, unidentified dandelion-like composites; (Ericaceae) *Rhododendron anthopogon* D. Don; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced], *Pedicularis oederi* Vahl, *P. roylei* Maxim., *P. pectinata* Wallich ex Benth., *P. rhinanthoides* Schrenk, *P. punctata* Decne.; (Labiateae) *Phlomis bracteosa* Royle ex Benth., *Nepeta podostachys* Benth., *Prunella vulgaris* L., *Thymus linearis* Benth. ex Benth.

DISTRIBUTION OF THE FAUNA

Distribution with altitude

The slopes of Mt Apharwat in the Pir Panjal range (Map 4 locality 1) show many of the more mesic kinds of habitat in which bumble bees occur in Kashmir. Differences in the distributions of the bumble bee species with altitude can be described from transect walks of the north-eastern flank of Apharwat (see the introduction on mate-searching behaviour of male bumble bees in Kashmir). These transects ran from Tangmarg at 1800 m in the Vale of Kashmir, through Gulmarg at 2700 m, to the peak of Apharwat above at 4143 m (13,592 ft). More than 2000 bumble bees were examined in the field along these transects during July, August and September 1985. Fig. 6 shows the records for each of the social species between the 500 ft contours of the 1 : 63,360 British Survey of India map (Oxford University Library). These patterns of distribution are similar to those found along the same transects in 1980 and 1986, and on other mountains around the Vale of Kashmir in all three years.

Away from the foot of the mountain, the middle of the Vale of Kashmir around Dal Lake (1500 m) is marshy and much of this area is used for the cultivation of rice. No bumble bees were found there. As the land slopes gently towards the mountains, terraces of rice give way on drier ground to apple orchards and higher still, near Tangmarg, to maize. Above Tangmarg, the lower coniferous forest (1900–2700 m) is dominated by *Pinus wallichiana* A.B. Jackson, with *Cedrus deodara* (Roxb. ex D. Don) G. Don near the lower margin. The forest is protected by law, although its lower edge now largely coincides with a pronounced increase in slope just above Tangmarg. The understorey is very disturbed and although few trees are felled, their branches are still collected for firewood. Flowers used by bumble bees are scarce in the lower forest (species listed in Table 5) but are more abundant around buildings and along roadsides. Bumble bee densities are very low, with *B. tunicatus* and *B. trifasciatus* the most abundant species both within the forest and around its lower edge.

Gulmarg (= 'flower-meadow', 2700 m) occupies a basin on a shoulder of the mountain. This natural, marshy meadow is grazed intensively by cattle, sheep and horses, yet the flowers from which bumble bees feed (Table 5) remain abundant. In the extensive wet areas of the meadow, *Prunella vulgaris* is a major nectar source and *Pedicularis punctata* a major pollen source for much of the summer. Large stands of the thistle *Cirsium falconeri*, which is often over 2 m tall, occur on disturbed slopes around the edges of the meadow. *Impatiens glandulifera* is abundant around water outflows from houses. The density of bumble bees is high (e.g. 89 bees/km, from 2.7 km transect, 14.ix.1986), with *B. asiaticus* and *B. tunicatus* the most abundant species, although there are fewer species than in the other zones (Fig. 6).

The upper coniferous forest is dominated in turn by *Pinus wallichiana* (2700 m), *Picea smithiana* (Wallich) Boiss. (2700–2900 m) and *Abies spectabilis* (D. Don) Mirbel (2900–3000 m). Prominent members of the shrub layer are bushes of *Sambucus wightiana* Wallich ex Wight & Arn. and *Euonymus hamiltonianus* Wallich. Flowers used by bumble bees (Table 5) are few, as in the lower forest. *Digitalis purpurea*, and more commonly *D. lanata*, are naturalised just above Gulmarg. Bumble bee density is low (23 bees/km, from 4.2 km, 14.ix.1986), with *B. pyrosoma* and *B. tunicatus* the most abundant species.

The lower slopes (3000–3200 m) of the sub-alpine

Table 5 Lists of the plants that were visited most frequently by foraging bumble bees on Mt Apharwat during 1985 and 1986 in the different altitudinal zones (LF, lower forest; GM, Gulmarg meadow; UF, upper forest; SA, subalpine; A, alpine; +, visited frequently; *, major food source).

Family	Binomen	Altitudinal zone LF	GM	UF	SA	A
Ranunculaceae	*Aconitum heterophyllum* Wallich ex Royle				+	
	Aconitum hookeri Stapf				*	+
Balsaminaceae	*Impatiens glandulifera* Royle	+	*			
Leguminosae	*Lupinus* sp.		+			
	Trifolium repens L.		+	+		
Caprifoliaceae	*Lonicera quinquelocularis* Hardw.				+	
Compositae	*Cirsium falconeri* (Hook. f.) Petrak		*	+	+	
	Cirsium wallichii DC.	*	+	+		
	Lactuca lessertiana (DC.) C.B. Clarke				+	+
	yellow dandelion-like composites				+	+
Ericaceae	*Rhododendron anthopogon* D. Don				*	
Oleaceae	*Syringa emodi* Wallich ex Royle				+	
Gentianaceae	*Swertia petiolata* D. Don			+	*	*
Scrophulariaceae	*Scrophularia pauciflora* Benth.				+	
	Digitalis purpurea L.		+			
	Digitalis lanata Ehrh.	+	+	*		
	Pedicularis oederi Vahl					+
	Pedicularis roylei Maxim.					+
	Pedicularis pectinata Wallich ex Benth.					+
	Pedicularis punctata Decne.	+	*	+		
Labiateae	*Phlomis bracteosa* Royle ex Benth.				+	
	Stachys sericea Wallich ex Benth.		+			
	Prunella vulgaris L.	+	*	+		
	Thymus linearis Benth. ex Benth.				+	+
	Salvia hians Royle ex Benth.				+	
Polygonaceae	*Bistorta vivipara* (L.) Gray					+

zone (Fig. 1) are dominated by species of *Salix*, *Betula utilis* D. Don and lilac, *Syringa emodi*. Large areas are strewn with boulders. Spaces between the rocks provide nest sites for bumble bees and refuges from grazing for *Scrophularia pauciflora*, which, despite its green flowers, is very attractive to bumble bees. Much of this zone is used as pasture for goats, sheep and cattle, especially in the more gently sloping area, known as Khilanmarg, that is immediately above the forest. Pasture areas have many bushes of *Euphorbia wallichii* Hook. f. and flowers of *Anemone obtusiloba* D. Don. The steeper middle slopes (3200–3400 m) are dominated by *B. utilis* and *Rhododendron campanulatum* D. Don. The upper slopes (3400–3800 m) are dominated by *R. anthopogon*, *Juniperus recurva* Buch.-Ham. ex D. Don and *Bergenia stracheyi* (Hook. f. & Thoms.) Engl. Overall, the subalpine zone has the largest number of bumble bee species (Fig. 6), although their total density (32 bees/km, from 4.2 km, 12.ix.1986) is less than at Gulmarg. The most abundant species throughout the subalpine zone is *B. rufofasciatus*.

The alpine zone (3800–4143 m) is marked by an absence of the low bushes of *R. anthopogon* and by the presence, at least in exposed areas, of a silver-grey mat vegetation with *Anaphalis triplinervis* (Sims) C.B. Clarke and species of *Leontopodium* (Edelweiss). *Bistorta vivipara* is conspicuous, but the major food-plants for bumble bees are species of *Pedicularis*, *Swertia petiolata* etc. (Table 5). The most abundant bumble bee species are *B. rufofasciatus* and *B. kashmirensis* (density of all bumble bees 31 bees/km, from 2.3 km, 12.ix.1986). These two species are closely similar in colour pattern and general appearance, but all of the individuals with this colour pattern that were caught visiting flowers of Compositae were of *B. rufofasciatus*, whereas those visiting *Aconitum hookeri* were all of *B. kashmirensis*.

The overall pattern in the distribution of the species' foraging activities with altitude on Mt Apharwat (Fig. 6) is very similar to that found on other mountains around the Vale of Kashmir (e.g. near Pahalgam and near Daksum). The overlaps in the species' altitudinal ranges on these mountains were more extensive than those measured along the floor of the Sind valley (Fig. 12). For instance, species such as *B. trifasciatus* and *B. tunicatus* are restricted to the lower end of the Sind valley (e.g. Kangan, 1900 m) and other species such as *B. rufofasciatus* and *B. keriensis* are restricted to the upper end (e.g. Sonamarg, 2700 m), although they have all been collected from the same meadow on Apharwat (2700 m). The Sind river runs from deep in the Great Himalaya to the Vale of Kashmir, so the slope of the valley floor is far less steep than the north-eastern flank of Mt Apharwat. It is more likely that individuals could wander or commute to forage outside their optimal altitudinal zones on Apharwat, simply because the zones are so much closer together horizontally. *B. simillimus* was common in the lower Sind valley (e.g. at Kangan, 1900 m) but was not found on Apharwat during 1980 or 1985. Three workers of this species were found at 3000 m on Apharwat in 1986.

In general, the distributions of bumble bee species are most likely to be governed by the combined effects of climate and of local levels of food resources (discussed in Williams, 1988, 1989). The environment in Kashmir is particularly complex, because the regional climate may be greatly modified locally by the effects of altitude and exposure (e.g. Troll, 1972). This is likely to have three principal direct effects on bumble bees. First, lower average temperatures at higher altitudes may increase thermoregulatory expenditure of energy by bumble bees, especially for queens, which must incubate their first brood alone in the spring. Second, a shorter annual season of temperatures above freezing point in the high mountains constrains the time available for colony development. However, daytime temperatures even in the alpine zone of Kashmir may be higher and more favourable than further north (e.g. in the Alps), although the day lengths are shorter in Kashmir. But third, at lower altitudes, bumble bees may actually suffer from heat stress. For instance, foraging activity by bumble bees (chiefly *B. trifasciatus* and *B. haemorrhoidalis*) at Patnitop (2000 m) in the Jammu foothills ceased during the warmest part of the day, between 10 a.m. and 5 p.m. (6–8.ix.1986), when the patches of *Impatiens glandulifera* and *Pteracanthus urticifolius* from which they were foraging were no longer in the shadows of the forest trees. The bumble bees could not be found visiting any other flowers elsewhere during these periods. A less pronounced trend towards bimodality in diurnal foraging patterns is well known for some temperate bumble bees (e.g. Heinrich, 1979; Willmer, 1983) and is also reported for the large carpenter bees of the genus *Xylocopa* at a subtropical lowland site (Abrol, 1987). In both of those situations, foraging activity by the bees was inversely related to air temperature and intensity of direct solar radiation, but was positively associated with nectar availability. At Patnitop, small and medium-sized anthophorine bees continued to forage from the same flowers throughout the day, so presumably at least some nectar was still available. A restriction of diurnal foraging periods for bumble bees is likely to reduce the daily rate of food supply to colonies and so slow their development within the limited foraging season. This has at least the potential to limit a species' distribution at the southern edge of its range.

In common with many other organisms, bumble bees tend to occur at higher altitudes in Kashmir than they do further north, but in zones with similar climate. *B. lucorum* is most abundant on Mt Apharwat around the upper edge of the montane forest zone (c. 3000 m) and is recorded from 2100–4600 m at other sites in Kashmir. Further north in the Alps, it is common on the forested middle slopes (1300–2600 m recorded by Pittioni, 1937). In cool temperate Britain, this species is common in virtually all of the available altitudinal zones down to sea level (0–1200 m).

Climate may also affect bumble bees indirectly through its effects on food resources. The lower parts of the valleys in Kashmir often appear to receive less rain or snow in summer than the mountain ridges. In some of the drier areas the availability of bumble bee food-plants in late summer may be very restricted and bumble bees are sometimes either absent or present at only very low density (e.g. at Baramula and Anantnag in the Vale of Kashmir). Food sources are also scant in the shade of the evergreen, coniferous forests on the hillsides. But higher in the mesic subalpine zone, the density of nectar-rich food-plants is often high and their diversity may be at its highest. In the alpine zone, the frequent freezing and overcast conditions throughout the summer are likely to reduce plant productivity and hence resources for bumble bees. The favourable balance of these climatic and food resource factors in the subalpine zone may help to account for its large number of species of bumble bees (Fig. 6).

Although the meadow at Gulmarg has much the highest density of bumble bees on Mt Apharwat,

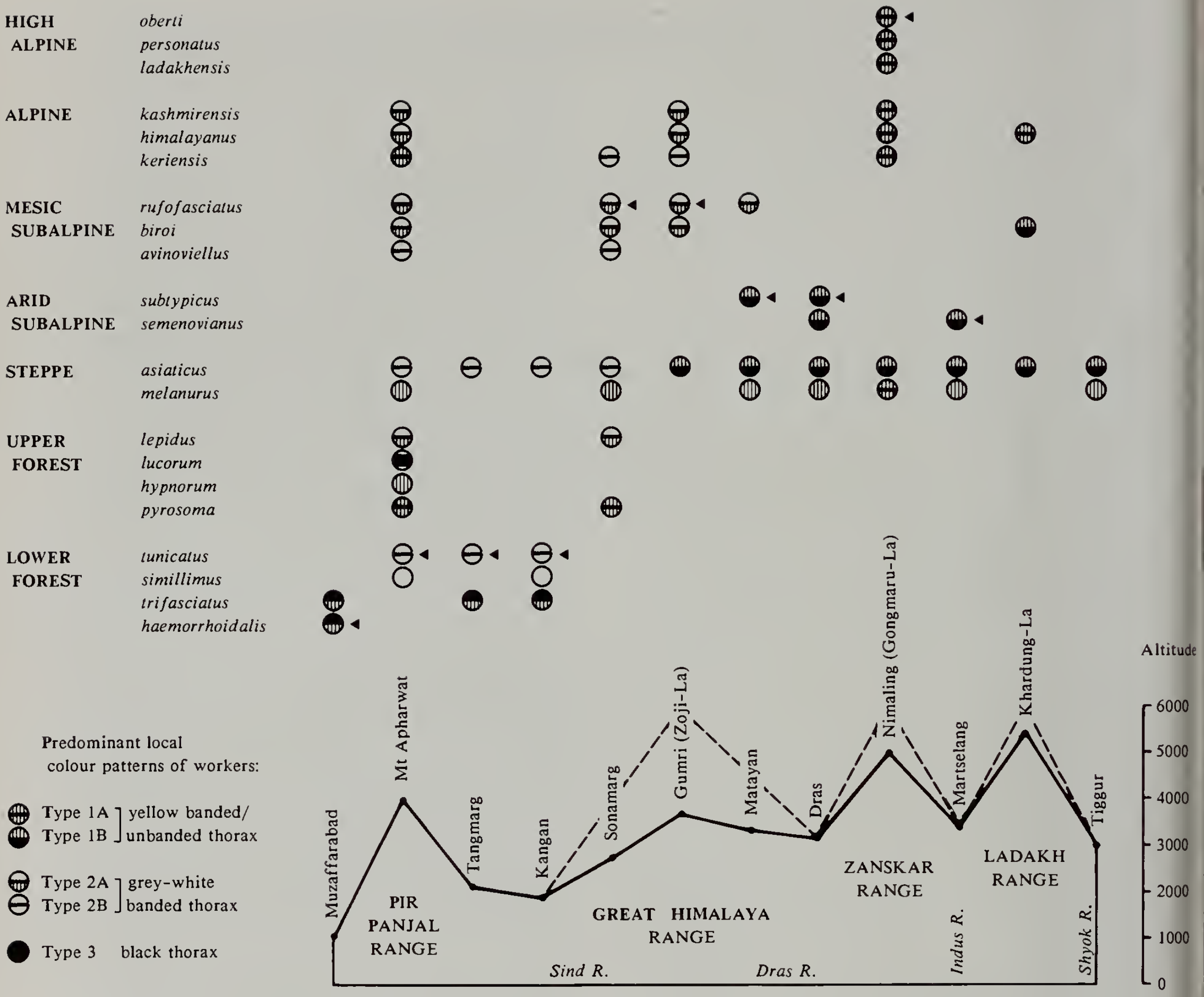


Fig. 12 Distribution of the social species of bumble bees (i.e. excluding species of the subgenus *Psithyrus*) and their local colour patterns across the Himalaya. Only the locally predominant patterns among the workers are represented. Triangles show the most abundant species at each locality. *B. lemniscatus* is not included for lack of information.

it has rather few species (Fig. 6). This may be partly because the abundance of food-plants is particularly uneven, although the relationship between diversity of food-plants and diversity of bees may not be straightforward (Williams, 1989). *Pedicularis punctata* and *Prunella vulgaris* are by far the most abundant of the food-plants used by bumble bees in the meadow. The meadow is often extensively flooded and some areas around streams are permanently marshy, although these plants are apparently tolerant of water-logged soil. Most of the more abundant species of bumble bees in the meadow, such as *B. tunicatus* and *B. pyrosoma*, are also among the most common species in the forest. Nests of both species have been found in the forest, but not in the meadow, so it may be that many of their foragers commute from nests in the forest to the richer resources in the meadow. *B. asiaticus* is unusual because it is both abundant on Gulmarg meadow and generally associated with open habitats.

The locality at the highest altitude in Kashmir from which I have collected a large sample of bumble bees is on Nimaling plain (4800 m). This is a high glacial valley, surrounded by large areas of arid alpine steppe that have very few if any bumble bees. Visits for 13 days in July 1980 and for three days in September 1986 found nine species of bumble bees (including the social parasite *B. (Psithyrus) branickii*) visiting the flowers of only a single plant species, *Caragana versicolor*. This plant forms low, thorny bushes on the old lateral and terminal moraines (Fig. 3), from which the glacier snout has retreated up the valley by about 10 km to the south-east. If the foragers do all genuinely use what appears to be a single food-resource, and there were no other obvious potential food-plants to be seen, then this situation deserves further study. It would follow from the application of competition-based ideas of 'community structure' to these bumble bees (e.g. Inouye, 1977) either that the flowers of *Caragana* are very variable in the accessibility of their rewards to the different bumble bee species, or that other factors are preventing the local assemblage of bumble bee species from reaching equilibrium by the local extinction of most of the species (cf. Williams, 1989).

Fig. 6 shows the narrower range of altitudes and habitats in which the males search for mates on Mt Apharwat, in comparison with the range of habitats in which the females forage. The possible relationship between the different kinds of male mate-searching behaviour and the different kinds of habitat is summarised in the introduction.

Distribution across the Himalaya

The distribution of bumble bees across the Kashmir Himalaya can be described from the samples collected at selected sites in the Pir Panjal, Great Himalaya, Zanskar and Ladakh ranges during August and September 1986. These data are supplemented with records from specimens collected at Nimaling in 1980 and with others examined in collections from Muzaffarabad (BMNH), from the Khardung-La above Leh (FA, ZI) and from Tiggur near the Nubra/Shyok confluence (BMNH). Together this covers a horizontal distance of about 430 km from west to east, at about 34° latitude. Fig. 12 shows the distributions of the bumble bee species in these samples and their locally predominant colour patterns.

The most widespread species in Kashmir are the steppe species *B. melanurus* and *B. asiaticus*. *B. asiaticus* shows a major change in colour pattern between Nigagar and Gumri in the Great Himalaya range, with some intermediate individuals present at Nigagar (see the discussion of variation of *B. asiaticus* in Kashmir). The alpine element in the fauna is also widespread between the Vale of Kashmir and Zanskar. Like *B. asiaticus*, *B. kashmirensis* and *B. himalayanus* show a pronounced change in colour pattern, but in this case the major transition in the thoracic pattern is to the east of Gumri (and to the west of Nimaling).

The principal boundary in the composition of the fauna is associated with the Great Himalaya range. This region of transition was studied in more detail between 9–11.viii.1986 in samples from Sonamarg, Nigagar, Baltal, Gumri, Matayan and Dras (a gradient-directed transect, see Map 4 & Table 1). The forest element is represented at Sonamarg, Nigagar and Baltal but, like the forest, it is absent to the north-east, beyond the Zoji-La (La = pass). There is also a large change in the subalpine element across the Great Himalaya. Of the subalpine species found on Mt Apharwat, *B. rufofasciatus* reaches across the Great Himalaya as far as Matayan, although *B. biroi* may be more widely distributed in Zanskar and Ladakh (Map 42). At Matayan, *B. rufofasciatus* occurs together with *B. subtypicus*, although *B. rufofasciatus* is no longer the most abundant species, as it is in the subalpine zones around the Vale of Kashmir. The three high alpine species found at Nimaling are distributed widely across the Tibetan massif but are apparently absent from the mountains around the Vale of Kashmir. This abrupt discontinuity in the faunal composition reflects the transition in climate and vegetation from the more mesic, wooded environment of the Vale of Kashmir to the arid (= xeric), steppe environment of the high Tibetan massif (Map 3). The environmental differences between these two regions in Kashmir are more extreme than those across the eastern Himalaya (Chang, 1981), where the Tibetan plateau is generally lower, more humid and dissected by wooded valleys. This is reflected in the distribution of bumble bees such as *B. rufofasciatus*, which penetrates much more deeply into Tibet in the east (Wang, 1982; BMNH).

A second boundary in the composition of the fauna is located on the outer slopes of the Pir Panjal range. The low altitude fauna has not been studied thoroughly here, largely for reasons of inaccessibility (see the comments on material examined). It is dominated by a lower montane forest element (*B. haemorrhoidalis* and *B. trifasciatus*). This includes many more species in the more humid foothills of the central and eastern Himalaya, where the effects of the monsoon are more pronounced.

From the limited amount of material available (BMNH, NMS, PW), the general pattern in the distribution of bumble bees across the Himalaya of Kashmir is similar to that found across the Himalaya of western Nepal (Table 6). The major difference is that the same arid subalpine element is not known to be represented in Nepal or in the adjacent parts of Tibet. The Kashmir-western Nepal region of the Himalaya spans about 1000 km, but shares a broadly similar pattern of climate and vegetation (see the maps in Schweinfurth, 1957). The pattern of vegetation formations is highly convoluted locally because it

Table 6 Distribution of the social bumble bees of Kashmir (i.e. excluding species of the subgenus *Psithyrus*) outside Kashmir. X – present in the regional lists from world summary grid-squares (see Map 1): AP, western Alps; AR, Armenia and the Caucasus; MG, northern Mongolia; TS, central Tien Shan; HK, Hindu Kush; NP, Nepal; GS, southern Gansu; BM, central Burma; TW, Taiwan.

	Region									
Habitat in Kashmir:	AP	AR	MG	TS	HK	Kashmir	NP	GS	BM	TW
High alpine				X		*oberti*		X		
						personatus	X	X		
						ladakhensis	X	X		
Alpine						*kashmirensis*	X	X		
						himalayanus				
		X	X	X	X	*keriensis*	X	X		
Mesic subalpine						*rufofasciatus*	X	X	X	
			X	X	X	*biroi*				
						lemniscatus	X	X		
						avinoviellus				
Arid subalpine					X	*marussinus*				
				X	X	*subtypicus*				
					X	*semenovianus*				
Steppe			X	X	X	*asiaticus*	X	X		
		X	X	X	X	*melanurus*	X	X		
Upper forest						*lepidus*	X	X		
	X	X	X	X	X	*lucorum*	X	X		
	X	X	X			*hypnorum*	X	X		
						pyrosoma	X	X		X
Lower forest					X	*tunicatus*	X			
						simillimus				
						trifasciatus	X	X	X	X
						haemorrhoidalis	X		X	

tends to follow contours, but throughout this region it consists essentially of bands parallel to the Great Himalaya (e.g. Map 3). So for bumble bees, as for the vegetation and for many other groups of organisms (e.g. Mani, 1986), the fauna apparently changes to a greater extent in a small distance across the Himalaya than it does along them. This supports the familiar idea that distributions are restricted less by the capacity of organisms to spread through a habitat than by their capacity to colonise a different kind of habitat (e.g. Fretwell & Lucas, 1970).

Distribution outside Kashmir

Only the broadest patterns in the distribution of bumble bees outside Kashmir can be discussed without an analysis of the distribution of all bumble bee species (in prep.). Table 6 summarises the distributions of the social bumble bees of Kashmir (i.e. excluding species of the subgenus *Psithyrus*) across some of the mountainous areas of Europe and Asia. The species are listed in a sequence to show their altitudinal distribution and habitat association within Kashmir (see Figs 6 & 12).

The alpine and high alpine species of Kashmir are primarily associated with the Tibetan massif (Table 6: reaching Nepal, Gansu). The distributions of *B. keriensis* and *B. oberti* also extend westwards and northwards through the Pamir to the Tien Shan ranges and, for *B. keriensis*, further to Armenia in the west and to the mountains of northern Mongolia in the north-east.

The subalpine and steppe species of Kashmir are principally associated with the arid mountains to the north in central Asia (Table 6: Hindu Kush, Alai-Tien Shan s.l.). There are also a couple of very widespread, cool temperate and upper montane forest species (*B. lucorum* and *B. hypnorum*). Species of the arid subalpine element are at the south-eastern limits of their distributions in Kashmir. Species of the steppe element are also more widespread in central Asia, but reach beyond Kashmir eastwards into the Tibetan massif. Together with the alpine species these correspond to the 'western hypsobiont element' described from the Himalayan butterfly fauna by Mani (1986).

The remaining species are found in and around the forests at lower altitudes and are more southern and eastern in their distribution outside Kashmir. They are either restricted to the western Himalaya (*B. tunicatus* and *B. simillimus*) or are at the western limit of their distributions (Table 6: reaching eastwards to Nepal and Taiwan). *B. haemorrhoidalis* and *B. trifasciatus* reach eastwards and southwards into the Oriental tropics in the mountains of northern Thailand. Together this group of eastern species corresponds to the 'eastern forest element' described from butterflies by Mani (1986).

Four species are narrowly endemic to the western Himalaya, *B. avinoviellus, B. himalayanus, B. tunicatus* and *B. simillimus*. It is possible that *B. himalayanus* may prove to be conspecific with the central Asian taxa *B. turkestanicus* and *B. marussinus* (see the comments on *B. marussinus* and *B. himalayanus*). The three remaining species are among the more plesiomorphic species within their respective species-groups. If they are relics of a relatively ancient bumble bee fauna that was once more widespread, then it now persists in a region that has been subject to some of the most active mountain building during the last few million years (see Bally, 1983; Mani, 1986). But although the western Himalaya may not appear to have been a particularly stable refuge in this period, the high relief could have provided some buffering against any climatic fluctuations by allowing altitudinal displacement of bumble bee populations.

Overall, the bumble bee fauna of Kashmir includes particularly few of the relatives of the European *B. hortorum* (only *B. trifasciatus*) or *B. pascuorum* (only *B. haemorrhoidalis*), but particularly many of the relatives of the European *B. lapidarius* (8 species of the subgenera *Sibiricobombus* and *Melanobombus*). This pattern (9% *Megabombus* + *Diversobombus* + *Thoracobombus* + *Orientalibombus* : 35% *Sibiricobombus* + *Melanobombus*, Kashmir fauna excluding *Psithyrus*) contrasts markedly with the representation of these groups in the fauna of the European Kalsbach Alps (31% : 6%, Pittioni, 1937), in the fauna of the whole of Europe (34% : 8%, Reinig, 1981) or in the fauna of the western Palaearctic (32% : 10%, Rasmont, 1983*b*).

Relationships between patterns at different spatial scales

Among the social bumble bees, those species that are more widespread world-wide are not generally found at more localities within Kashmir (Fig. 13, which excludes the species of the subgenus *Psithyrus*, Kendall coefficient of rank correlation 0.08, $P > 0.5$ n.s.). It is possible that these data might not be representative because the sampling effort was far from uniform at both spatial scales and the sites in Kashmir were not randomly located but selected by kind of habitat and for ease of access. Nonetheless, there is pattern in the data insofar as species with similar habitat associations (Figs 6 & 12) do tend to occur closer together in Fig. 13. One interpretation is that this pattern in Fig. 13 may show a common limiting effect within the groups of species with similar habitat requirements, which could be just a consequence of the limited availability of the most suitable kinds of habitat for these species at both spatial scales.

From a study of British bumble bees, patterns in local distributions appear to be related to how close the species are to the centres of their world-wide distributions (Williams, 1988). Among the Kashmir fauna, those species that are nearer to the centres of their world-wide distributions (from Maps 5–62: *B. avinoviellus, B. himalayanus, B. melanurus, B. tunicatus, B. asiaticus, B. semenovianus, B. keriensis* and *B. simillimus*) do also tend to occur at more localities within the country (Maps 5–62; Fisher-Pitman randomisation test, $W = 181$, single-tailed $P < 0.01$, see Krauth, 1988). More precisely, those species that are nearer to the centres of their distributions in Britain have been found in a broader range of kinds of habitat. For the fauna of Kashmir, this greater breadth of habitat use for those species that are nearer to the centres of their world-wide distributions is apparent in the greater altitudinal ranges of these species within the country (excluding single altitude records of *B. oberti* and *B. lemniscatus*, Fisher-Pitman randomisation test, $W = 18400$, single-tailed $P < 0.05$).

Fig. 13 also appears to contain information as to how close the species are to the centres of their world-wide distributions. For these data in which the variance is similar in the log(world) and log(kashmir) distribution values, the central/marginal position of a species appears to be related to log(kashmir)-log(world). Since all species tend to occupy more localities nearer to the centres of their distributions, then if the more widespread species world-wide were generally found at more localities within comparable parts of their distributions, perhaps the deviation of the Kashmir species from any underlying positive relationship in Fig. 13 might show some influence of how far Kashmir is from their centres of world-wide distribution.

The relationship between distribution patterns and patterns of local abundance found among British bumble bees (Williams, 1988) is not consistently evident in the samples from Kashmir. Those species that were chosen from the maps to

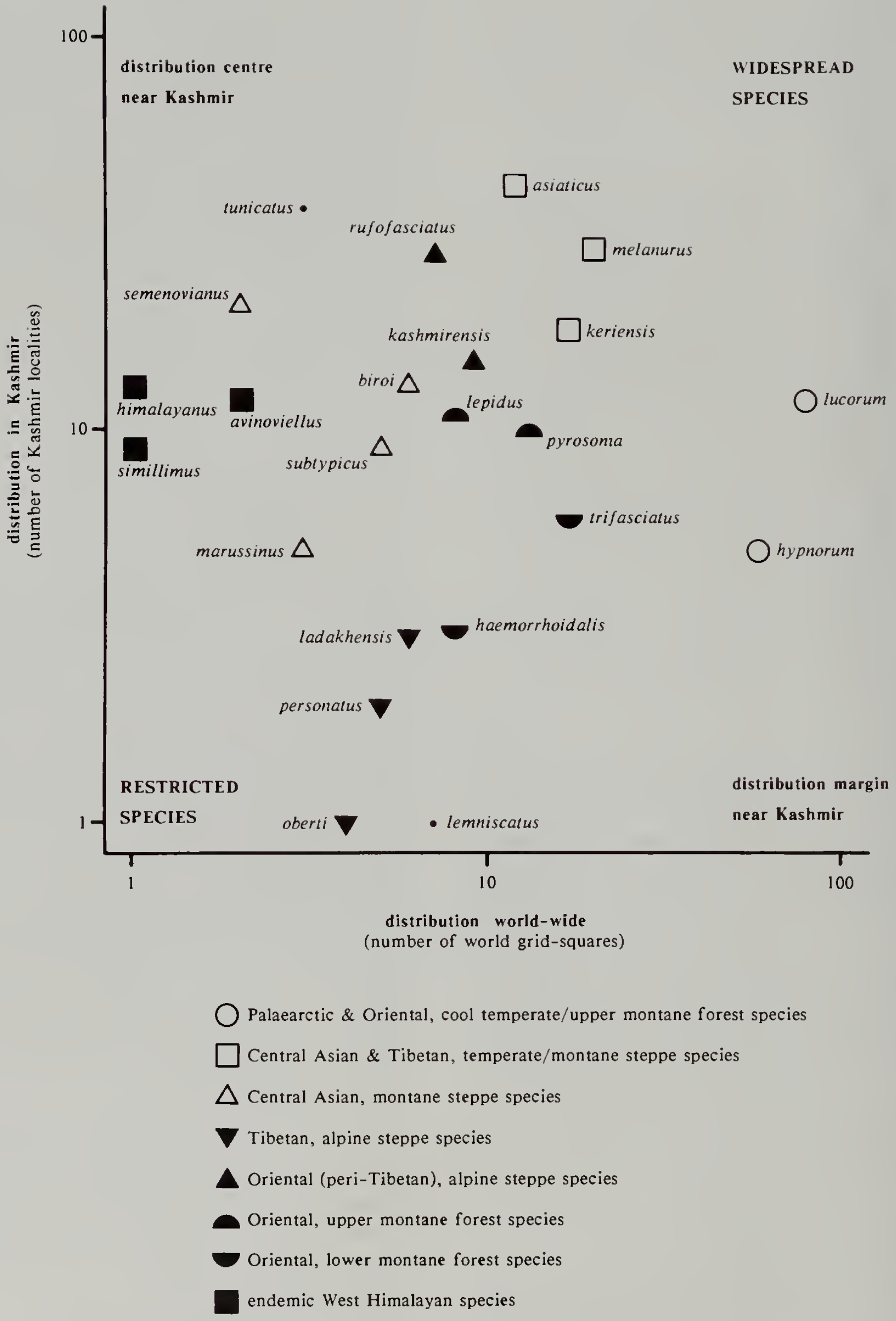


Fig. 13 Plot of how widespread the species of social bumble bees (i.e. excluding species of the subgenus *Psithyrus*) are within Kashmir against how widespread they are world-wide (logarithmic axes). Data are taken from occupancy of the number of localities within Kashmir (see Map 4) and from the number of world summary grid-squares (see Map 1) respectively. The distributions of *B. tunicatus* and *B. lemniscatus* are anomalous.

be nearer to the centres of their world-wide distributions in Kashmir do not appear to be generally more abundant locally in these samples (local abundance for a species estimated as the total numbers of individuals examined from Kashmir / numbers of localities in Kashmir, Fisher-Pitman randomisation test, $W = 145$, single-tailed $P = 0.19$ n.s.). However, there is still a tendency for the more widespread species within Kashmir to be more abundant locally (Kendall coefficient of rank correlation 0.29, single-tailed $P < 0.025$). It is possible that even if there were a relationship with the world-wide pattern, it may have been obscured in these data because the later collections at least were strongly biassed against including many specimens of the common species from each site, whereas the rare species were deliberately sought.

Relationships between the patterns of distribution at different spatial scales form the basis of a simple model for the interaction of those ecological factors that are most likely to govern bumble bee distributions (discussed in Williams, 1988, 1989). It follows from this that where some disturbance of sites causes a major reduction in food availability, it is the species that are nearest to the centres of their world-wide distributions that are most likely to persist. This may provide one explanation for the observation that *B. tunicatus* and *B. asiaticus* are the species that are often found alone in severely over-grazed areas around the edge of the Vale of Kashmir and in the Sind valley.

COLOUR PATTERNS OF THE KASHMIR FAUNA

The colour patterns of bumble bees often vary greatly among individuals of one species (e.g. Fig. 11), but may be closely similar between individuals of unrelated species where these species occur together (Fig. 12; see e.g. Vogt, 1909, 1911; Sakagami & Yoshikawa, 1961; Tkalců, 1968*b*, 1989; Pekkarinen, 1979; Plowright & Owen, 1980). Genetic determination of characteristics of the colour pattern with simple Mendelian inheritance has been demonstrated for the North American *B. melanopygus* and *B. rufocinctus* (Owen & Plowright, 1980; Plowright & Owen, 1980; Owen, 1986). But in the face of such marked regional convergence, several authors have questioned whether variation among colour patterns of individuals within a population is always determined genetically, or whether it is perhaps more often determined directly by environmental factors, such as diet, temperature or humidity during development (e.g. Vogt, 1909, 1911; Reinig, 1935; Pittioni, 1942, 1943).

The pubescence of bumble bees develops during the pupal stage and the colours appear soon after the adults emerge from their cocoons. Adult queen and worker bees invest much time and energy ensuring that the conditions in the nest remain nearly constant, for instance by incubating brood or by fanning air over the nest to regulate temperature as necessary (e.g. Heinrich, 1979). Hence the brood is shielded from many of the possible environmental effects on colour pattern during its development, so colonies usually produce individuals with relatively homogeneous colour patterns. However, if a nest is exposed and moved to a nest box, unusual colour patterns are more often found among the adults that subsequently emerge from pupation (pers. obs.).

The few examples of pronounced caste dimorphisms show that colour patterns are not solely determined by genes, but must also be influenced by the environment. Two examples have been described previously from subtropical environments (*B. ephippiatus* from the mountains of Costa Rica, see Owen & Plowright, 1980; *B. festivus* from the eastern Himalaya, see Ito *et al.*, 1984), in which workers and males from the same colonies share similar colour patterns that differ strongly from those of the queens. Similar differences exist within species of the *rufofasciatus*-group from Kashmir (see Plate 1). For *B. pyrosoma*, males usually also differ in that they have the pubescence predominantly yellow (Figs 424, 427, 430), a characteristic that can be regarded as sex-linked (see Stiles, 1979). But colour variation among the females from Kashmir appears to be related to body size (which increases through Figs 426, 428, 429, 425, see the comments on *B. pyrosoma*) and so to larval food intake. From the material available it seems most likely that the white-tailed queens from Kashmir belong to the same population as the nominal taxon *B. friseanus* from Yunnan (synonymised with *B. pyrosoma* s.l.). These queens from Yunnan have the pubescence of terga IV-V red, so they closely resemble their own workers from Yunnan and also many of the workers from Kashmir. Thus caste dimorphism in colour pattern may exist in only part of the population of *B. pyrosoma* s.l.

Variation of *B. asiaticus* in Kashmir

The *asiaticus*-group is particularly well represented in collections for an investigation of the variation in the colour pattern of the pubescence.

In Kashmir, two principal nominal taxa occur on opposite sides of the Great Himalaya range (Map 48), one with an unbanded yellow thorax (Figs 371–376), the other usually with a black band between the wing bases and an otherwise grey-white thorax (Figs 383–391). These nominal taxa are believed to be parts of a single species (see the comments on *B. asiaticus*).

The basis of this colour variation can be examined where the regional colour patterns occur together. At a few sites at the upper end of the higher valleys in the Great Himalaya, the *B. asiaticus* are not uniformly of one or other of the two principal colour patterns, but instead many individuals show a variety of combinations of their differing character states (Figs 377–382). The largest sample with this kind of variation was collected by F. Schmid from Lal Pani in the upper Kishanganga valley between 2–3.ix.1953 (BMNH: Table 7). This is likely to be a relatively unbiassed sample insofar as he specialised in collecting Trichoptera and not particular bumble bee taxa. I have also collected a small sample that shows similar variation, from Nigagar in the upper Sind valley (9.viii & 17.ix.1986, PW). The occurrence of the black tail-colour state (Figs 379–381) at both of these localities is curious. It is not known for individuals from the adjacent regions of Ladakh or the Vale of Kashmir, although it is common in parts of the Hindu Kush ranges (BMNH).

The ability of simple population genetic models to account for the observed patterns of variation among the specimens from these boundary sites can be tested if certain assumptions are made. Three aspects of the variation are chosen because they appear to be among the most important elements of the bees' colour pattern as they are viewed flying among flowers. It is assumed initially that each character shows either of two states and that these are each determined by one of a pair of alleles at a single locus. In fact the three characters selected do not show entirely discrete states. However, the minority of intermediate specimens from the possible hybrid zone can be assigned to these states for a preliminary analysis (Table 7), at least until further information on modifier effects is available.

Table 7 Numbers of individuals of *B. asiaticus* collected by Schmid from Lal Pani 2–3.ix.1953 with each combination of states of three characters of the colour pattern of the pubescence. The scoring was simplified prior to analysis in order to present discrete states despite some limited intergradation. The black thoracic band is deemed to be present if it appears well defined from the dorsal aspect. The pale colour 'white' includes very pale cream. The 'tail' colour is deemed to be red if the pubescence of at least two of the apical terga is predominantly red.

Thoracic band	Pale bands	Tail colour	Females	Males
present	white	red	7	1*
absent	white	red	–	1
present	white	black	2	1
absent	white	black	1	–
present	yellow	black	3	34
absent	yellow	black	–	13
present	yellow	red	9	37
absent	yellow	red	–	5**

* *B. callophenax* of Richards, not of Cockerell
** *B. longiceps* Smith

Table 8 Association between pairs of character states of the colour pattern among the males of *B. asiaticus* from Lal Pani (see Table 7). None of these comparisons shows significant association (chi-square two-sample test, all comparisons $P>0.05$).

		Pale bands		Tail colour	
		white	yellow	red	black
Thoracic band	present	2	71	38	35
	absent	1	18	6	13
Tail colour	red	2	42		
	black	1	47		

There is no association between the states of the three colour characters among individuals from the top of the Kishanganga valley (Table 8). This apparent independent assortment of the characters shows an absence of the disequilibrium (e.g. Mallet, 1986) that would be expected if gene flow across the coincident character clines in the hybrid zone were large. Hybrid zones are expected to be captured by linear habitat features where population density is particularly low (e.g. Mallet, 1986; Hewitt, 1988). For *B. asiaticus* in Kashmir, this role may be fulfilled by the high ridges and passes of the Great Himalaya range. For instance, where the upper Sind valley reaches the main ridge of the Great Himalaya just above Nigagar, the valley floor rises abruptly by about 700 m at the Zoji-La pass. My small samples from either side of Nigagar, at Sonamarg (2700 m) and above Gumri (3700 m), each consist of material with a single colour pattern (i.e. the alleles may be nearly fixed), so the hybrid zone at the top of the Sind valley may be less than 16 km wide. Such a narrow cline is consistent with the interpretation that there is little gene flow across the hybrid zone at the top of the Kishanganga valley (Table 8). The hybrid zone at the top of the Kishanganga may, nonetheless, be much broader (Map 48, see the comments on variation within Kashmir for *B. asiaticus*).

Table 9 Observed numbers of individuals of *B. asiaticus* from Lal Pani with each state of three colour pattern characters (see Table 7), together with the expected numbers from simple genetic models. Frequencies from a small sample (n = 20) from Nigagar are included for comparison. Deviation from model significant at $P<0.05$ *, $P<0.001$ ***, or not significant ns.

		Observed:		**Expected:**	
		females (diploid)	males (haploid)	females – no dominance	females – simple dominance
Thoracic band	present	21	73	17	[est(p) = 73/92] 21
	absent	1	19	5	[est(q) = 19/92] 1
Frequency (absent) Lal Pani		0.05	0.21		
[Frequency(absent) Nigagar		0.00	0.66]		
(Chi-square one-sample test, df = 1)				(4.14)	(0.00)
Probability that deviation of observation from expectation is due to chance				$P<0.05$ *	$P>>0.05$ ns
Pale bands	white	10	3	1	[est(p) = 3/92] 1
	yellow	12	89	21	[est(q) = 89/92] 21
Frequency (yellow) Lal Pani		0.55	0.97		
[Frequency (yellow) Nigagar		0.50	0.66]		
(Chi-square one-sample test, df = 1)				(84.86)	(84.86)
Probability that deviation of observation from expectation is due to chance				$P<<0.05$ ***	$P<<0.05$ ***
Tail colour	red	16	44	11	[est(p) = 44/92] 16
	black	6	48	11	[est(q) = 48/92] 6
Frequency (black) Lal Pani		0.27	0.52		
[Frequency (black) Nigagar		0.14	0.33]		
(Chi-square one-sample test, df = 1)				(4.55)	(0.00)
Probability that deviation of observation from expectation is due to chance				$P<0.05$ *	$P>>0.05$ ns

The frequency of alleles can be estimated and the dominant allele can be determined from the frequencies of the character states, because although female bumble bees are diploid, the males are usually haploid (see Plowright & Pallett, 1979). The frequency of the character states among males in the large sample from Lal Pani is assumed to be representative of the allele frequencies in that local part of the population (which assumes that even if the material was collected in the proximity of only a very few colonies, it still represents a random sample of the local gene pool). These frequencies may differ at other localities in the Kishanganga valley or at Nigagar, so these samples cannot be combined for analysis. If there is simple, complete dominance by one of the two alternative alleles at each locus, then the frequencies of character states should differ between males and females, with higher frequencies of expression for the recessive allele among males. The higher frequencies among males of the lack of a black thoracic band, of yellow pale bands and of black 'tails' at both Lal Pani and Nigagar (Table 9) are consistent with their determination by recessive alleles. Furthermore, the frequencies of characters among males can be used to calculate the frequencies among females that would be expected if there were no dominance (which might result from Hardy-Weinberg equilibrium with co-dominance of both alleles, or from some mechanism other than straightforward Mendelian genetics). These calculated frequencies are found to differ significantly from those observed for all three characters (Table 9).

The observed frequencies of the states of the black thoracic band and of the tail colour among females are consistent with those expected from the Hardy-Weinberg equilibrium model with simple, complete dominance between two alleles (Table 9). However, this is rejected for the pale band colour character, the distribution of which was not consistent with the dominance-free model either. It has to be noted that the chi-square one-sample test is not reliable when an expected frequency is less than 5 (e.g. Siegel, 1956), but the values of chi-square that result here are so large (84.8, df = 1) that the conclusion that the model should be rejected is unlikely to be altered. The reason for the failure of the models must be that their assumptions are violated. In addition to those mentioned above, assumptions of the equilibrium model include insignificant dispersal, random mating and unselective predation.

Firm conclusions as to the genetic basis of the patterns of colour variation among these bumble bees cannot be drawn without breeding experiments. This would allow ideas of the pattern of inheritance to be tested, although this is not particularly easy with bumble bees (but see Owen & Plowright, 1980). However, the pattern of variation for two out of three of the characters that have been analysed is consistent with simple genetic models. It is therefore also consistent with the assumption that individuals with these colour patterns are interbreeding as parts of a single population and a single biological species. Thus local climate or diet does not appear to be the proximate factor governing the close convergence in colour pattern between this species and the regionally covarying groups of species on either side of the Great Himalaya.

Convergent colour patterns

It is noticeable that only a few of the possible colour patterns are actually found among bumble bees world-wide, given the range of colours shown by the pale pubescence of bumble bees and the observed patterns of disposition of bands of pale and black pubescence on their bodies (Plowright & Owen, 1980; BMNH, PW). For instance, at least half of all species of bumble bees have some individuals with a 'red-tailed' colour pattern. Other common elements in the colour pattern are a band of black hairs on the thoracic dorsum between the wing bases, and a black band on tergum III. The most widespread colour pattern of the dorsal pubescence among all bumble bees of the world appears to be for the thorax to be yellow with a band of black hairs between the wing bases and for the gaster to be yellow – black – red, from base to apex (cf. Figs 233–235, 242, 243, 298–300, 317, 318, 377, 378, 382, 388, 393, 407, 412–416, 426).

The three principal regions of Kashmir have groups of bumble bee species with characteristic colour patterns of the dorsal pubescence (Fig. 12):

(1A) In the high alpine zone of Ladakh, the most common colour pattern of the pubescence is for the thorax to have yellow transverse bands anteriorly and posteriorly, with a black band between the wing bases. The gaster is yellow (terga I-II) and red (terga III-V), although often with a narrow black band between them (basal quarter or less of tergum III).

(1B) At lower altitudes in the arid steppe of Ladakh, the common colour pattern is for the pubescence of the thoracic dorsum to be uniformly yellow and for the gaster to have a yellow band (terga I-II yellow, or just tergum I yellow, or terga I-II completely black) – black (at least tergum III) – red (usually terga IV-V).

(2A) Around the Vale of Kashmir, above the forests, the most common pattern is for the pubescence of the thoracic dorsum to be grey-white with a black band between the wing bases. The gaster is grey-white (tergum I) – yellow (usually tergum II) – red (terga III-IV, sometimes with white on terga IV-V).

(2B) In the Vale of Kashmir and the surrounding upper montane forest, the common colour pattern is banded and white as for type 2A, but the gaster lacks any yellow and is grey-white (tergum I, sometimes tergum II) – black (at least tergum III) – red (usually terga IV-V).

(3) In the lower montane forests of the Jammu foothills, the common colour pattern is for the pubescence of the thorax to be black and for that of the gaster to be yellow (terga I-II) and red (terga III-V), but without an obvious black band.

The type 1A colour pattern deviates only slightly from the widespread bumble bee pattern of three yellow bands and a red 'tail' by the replacement of much of the black on tergum III by red. This type 1A pattern is otherwise most predominant among individuals from the Pyrenees in Europe.

The type 1B pattern differs from the widespread pattern principally in the absence of a black band on the thorax, although it retains an extensive black area on the gaster. It is predominant in the Hindu Kush and occurs elsewhere in the Caucasus (*B. (Melanobombus) lapidarius*) and quite independently in South America (*B. (Fervidobombus) bellicosus* Smith).

The type 2A pattern differs from the widespread pattern by a change in the pale pubescence from yellow to grey-white on all but tergum II. The type 2A pattern is perhaps most predominant in Kashmir, but is also found around the southern and eastern margins of the Tibetan massif.

The type 2B pattern completes the transition of all of the yellow pubescence of the widespread pattern to grey-white. Individuals with this colour pattern occur widely in the Himalaya, the central Asian mountains and westwards in the Caenozoic mountains of southern Europe to as far west as the Alps (*B. (Pyrobombus) brodmannicus*) and the

Atlas mountains of North Africa (*B. lapidarius*). Males from populations with the type 2B pattern often retain the common banded yellow pattern (e.g. *B. wurflenii* and *B. lapidarius* from the Caucasus, *B. brodmannicus* from the Alps, *B. lapidarius* from the Atlas, BMNH). A variant of the type 2B pattern has tergum II or terga I-II dark chocolate-brown. This is seen in the Himalaya only among the males and workers of *B. tunicatus* (Figs 348, 349, 351, 352, 354) and *B. simillimus* (Figs 418, 420, 421), but it is also known from the Caucasus mountains for *B. (Thoracobombus) mlokosievitzii* Radoszkowski (BMNH, PW).

The type 3 pattern differs from the widespread pattern by the replacement of the pale pubescence on the thoracic dorsum by black and by the reduction of the black band on the gaster. In the western Himalaya individuals with this pattern are restricted to the outer foothills. Further east in Uttar Pradesh the same pattern is shared by *B. (Alpigenobombus) breviceps* and *B. (Pyrobombus) rotundiceps*.

So what is responsible for the apparent constraints on the range of bumble bee colour patterns that are actually observed? Why do these colour patterns appear to have converged especially closely among many species within each geographical region? These species are often not closely related, as shown by differences in their male genitalia. Colour pattern had no effect on acceptance of females by patrolling males of British *B. pratorum* (L.) (Free, 1971). Stiles (1979) suggested that colour affects radiative properties that may be crucial to thermoregulation in extreme climates. Sakagami & Ito (1981) challenged this interpretation of sexual dimorphism in colour pattern, because the two faunas compared by Stiles were dominated by different groups of species. Within each of these subgenera, *Fervidobombus* and *Pyrobombus*, no regional trends were found. However, there may be differences in the kind of habitat and in mate-searching behaviour between the species of these two groups that could also affect the relative advantages of the two kinds of colour patterns. The peculiar behaviour of males of some species of the subgenus *Fervidobombus* has been described by Lloyd (1981) and by Villalobos & Shelly (1987). It could be that many of these differences between the two groups, including differences in colour pattern, are each related to an underlying difference in physiology that is linked to their regional patterns of distribution more directly.

Many species of bumble bees commonly produce individuals that are entirely black, but these are most often predominant in tropical environments (Franklin, 1913). These species include *B. (Rufipedibombus) rufipes*, *B. (Megabombus) melanopoda* Cockerell and workers and males of *B. (Senexibombus) senex* Vollenhoven in the East Indies (BMNH), and *B. (Fervidobombus) brevivillus* Franklin, *B. (Fervidobombus) niger* Franklin [= *B. atratus* Franklin, preoccupied name], *B. (Fervidobombus) pullatus* Franklin and *B. (Fervidobombus) morio* (Swederus) in South America (BMNH, PW). An extensively black body is likely to have a lower reflectance even in the infra-red part of the spectrum and so should have a higher rate of approach to thermal equilibrium with the environment by an exchange of long-wave radiation. This may be an advantage to actively foraging bumble bees in a warm environment, because they produce a lot of excess heat from the flight muscles and so might otherwise suffer from heat stress. The subtropical black bees listed above may often be forest-dwelling. In the shade they can escape the additional problem of rapid overheating that could arise from an equally efficient absorption by black pigments of the short-wave radiation in direct sunlight. So this likely advantage of the black pubescence for bees foraging in a shaded warm environment may account for why the type 3 pattern, with a black thorax, the source of the endogenous heat, predominates among bumble bees at the lowest altitudes at which they occur in Kashmir (Fig. 12). It is very noticeable that near their lower altitudinal and latitudinal limits in Kashmir these bees (*B. trifasciatus* and *B. haemorrhoidalis*) forage particularly both in the shade and during the cooler periods of the day (see the discussion of the distribution of the fauna with altitude). However, further south in their distributions in South East Asia, these same species have extensively orange-brown colour patterns of the thoracic pubescence (Fig. 11). More information is needed on the foraging behaviour of these bees in South East Asia, where there is a tendency among the few large nocturnal bees and wasps to have an orange-brown colour pattern (M. C. Day, pers. comm.; Roubik, 1989). There is also clearly a need for measurements of the radiative properties of bumble bee colour patterns in general.

Male bumble bees that patrol in the higher forest on Mt Apharwat tend to be almost uniformly bright yellow (Fig. 6 and see the comments on *B. pyrosoma*, *B. lucorum* and *B. hypnorum*). This may also be true of those males that patrol in forests, but not in open habitats, at higher latitudes (see Pekkarinen, 1979: fig. 7, cf. Løken, 1973: fig.2). In contrast to black, a pale, highly reflective body colour should reduce the rate of approach to thermal equilibrium with the environment by an exchange of long-wave radiation, so that following an active warm-up, a sufficiently high excess thoracic temperature for flight can be reached quickly and maintained in a shaded cool environment. In contrast, males of those species that patrol in the forests at low altitudes, in open areas outside the forest or in a broad range of habitats in Kashmir tend to be darker and share the colour pattern of the females (Fig. 6). Uniform bright yellow may be disadvantageous in open areas beyond the forest, for instance in alpine and arctic zones, because it is very conspicuous to predators. This could be a particular problem for the more sedentary 'perch and sprint' males (e.g. *B. asiaticus* and *B. rufofasciatus*, see the introduction on mate-searching behaviour of male bumble bees in Kashmir) and those males that aggregate at nest entrances (which includes several species of *Fervidobombus*, e.g. review by Schremmer, 1972; Lloyd, 1981; Villalobos & Shelly, 1987). Yet the most uniformly light-coloured female bumble bees in Kashmir, which belong to the type 1A pattern-group, are found at the highest altitudes sampled for bumble bees, in Ladakh. This trend towards lighter colours in cooler environments is the reverse of that described by Pekkarinen (1979) from European species.

Regional convergences in the finer details of the colour pattern between bumble bee species are likely to be the result of selective predation. Predators with perception of colour and great visual acuity, perhaps certain birds, may avoid the familiar common colour patterns of these insects because the females can inflict a painful sting, and preferentially attack any individuals with unusual colour patterns. This kind of selection could bring about Müllerian mimicry among the colour patterns on the dorsa of the females (Plowright & Owen, 1980) and Batesian automimicry by the colour patterns on the dorsa of the stingless males (Stiles, 1979). The putative models for this process would be the colour patterns of the females of the most abundant species. In Kashmir, these species tend to be regionally restricted and relatively invariant in their colour patterns (type 1A, *B. oberti*, Figs 392, 393; type 1B, *B. semenovianus*, Figs 397, 398, 400, 401; type 2A, *B. rufofasciatus*, Figs 431, 432, 434, 435, 438; type 2B, *B. tunicatus*, Figs 350, 353; type 3, *B. haemorrhoidalis*, Figs 279, 280; see Fig. 12). Many of the mimics occupy the middle classes of abundance, but are often more widespread among the regions of Kashmir. These species covary in their colour patterns among the regions so that they show the protective livery of the local model (e.g. *B. avinoviellus*, Figs 232–241; *B. himalayanus*, Figs 242–253; *B. kashmirensis*, Figs 295–310; *B. lepidus*, Figs 327, 328, 330, 331, 333, 334; *B. biroi*, Figs 335–346; *B. asiaticus*, Figs 371–391).

A subtle difference between the colour patterns of *B. kashmirensis* and *B. rufofasciatus* could be interpreted as further circumstantial evidence in support of the mimicry hypothesis for colour convergence. Workers of these two species appear to be identical (type 2A colour pattern) when they are seen manoeuvring slowly from flower to flower in the alpine and subalpine zones of the mountains around the Vale of Kashmir. Most workers of *B. rufofasciatus* have the hairs of gastral terga III-IV almost uniformly red and those of tergum V uniformly white (Fig. 435). The *B. kashmirensis* from the same region often have all three terga (III-V) covered with hairs that are red at the base, but which become more extensively white-tipped towards the apex of the gaster (Fig. 303). This achieves the same white-tailed effect as for *B. rufofasciatus*, because the apex of the gaster curves slightly towards the ventral for bumble bees.

Colour variation within many of the bumble bee species of Kashmir does appear to be much greater than within the bumble bee species of Britain, or even within the more variable species of the Alps. This may be blamed on taxonomic 'lumping' in this review. But if bumble bee colour patterns have converged into separate and distinctive mimetic groups within each of the neighbouring regions of Asia, then the position of Kashmir at the frontier between the large and divergent Oriental and Palaearctic faunas (which are still to some extent separated even inside Kashmir by the divide of the Great Himalaya) may account in part for the great diversity of colour pattern within some of the Kashmir species.

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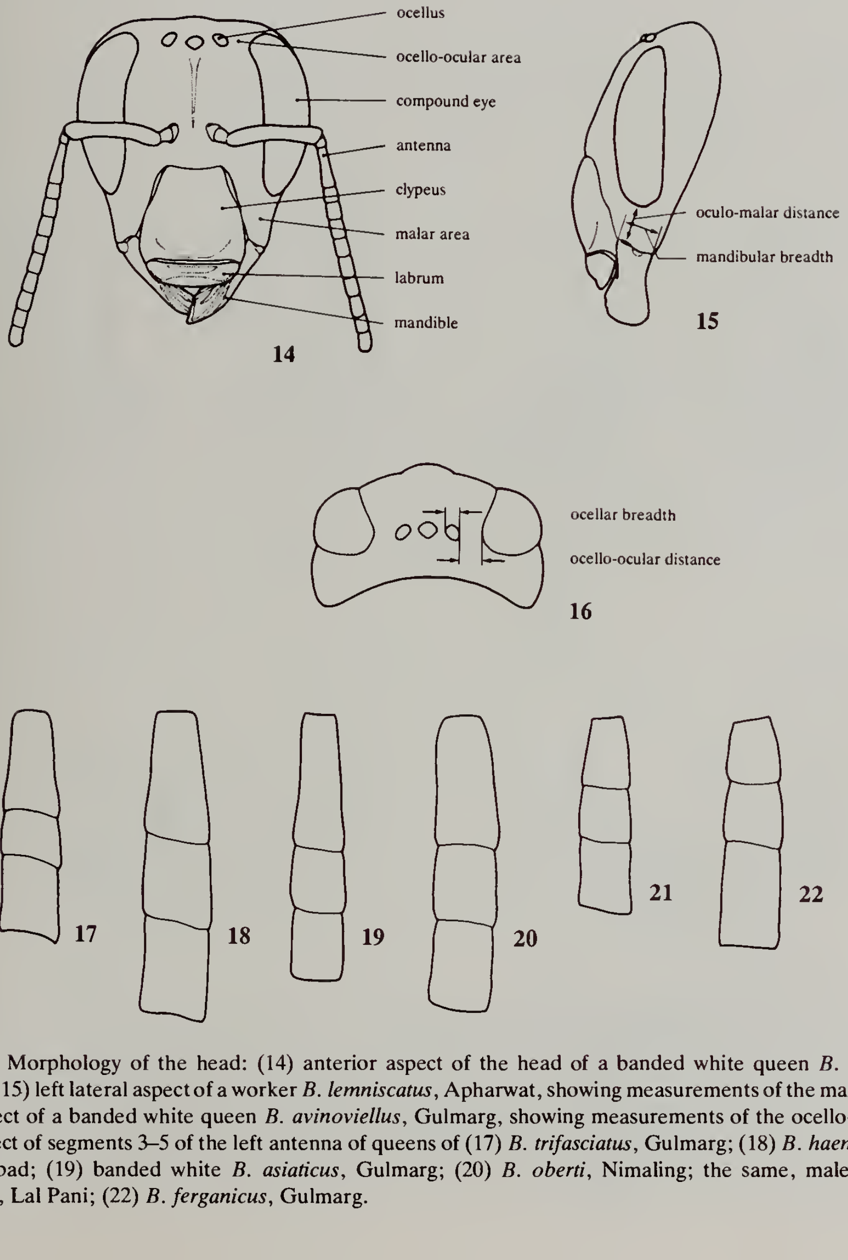
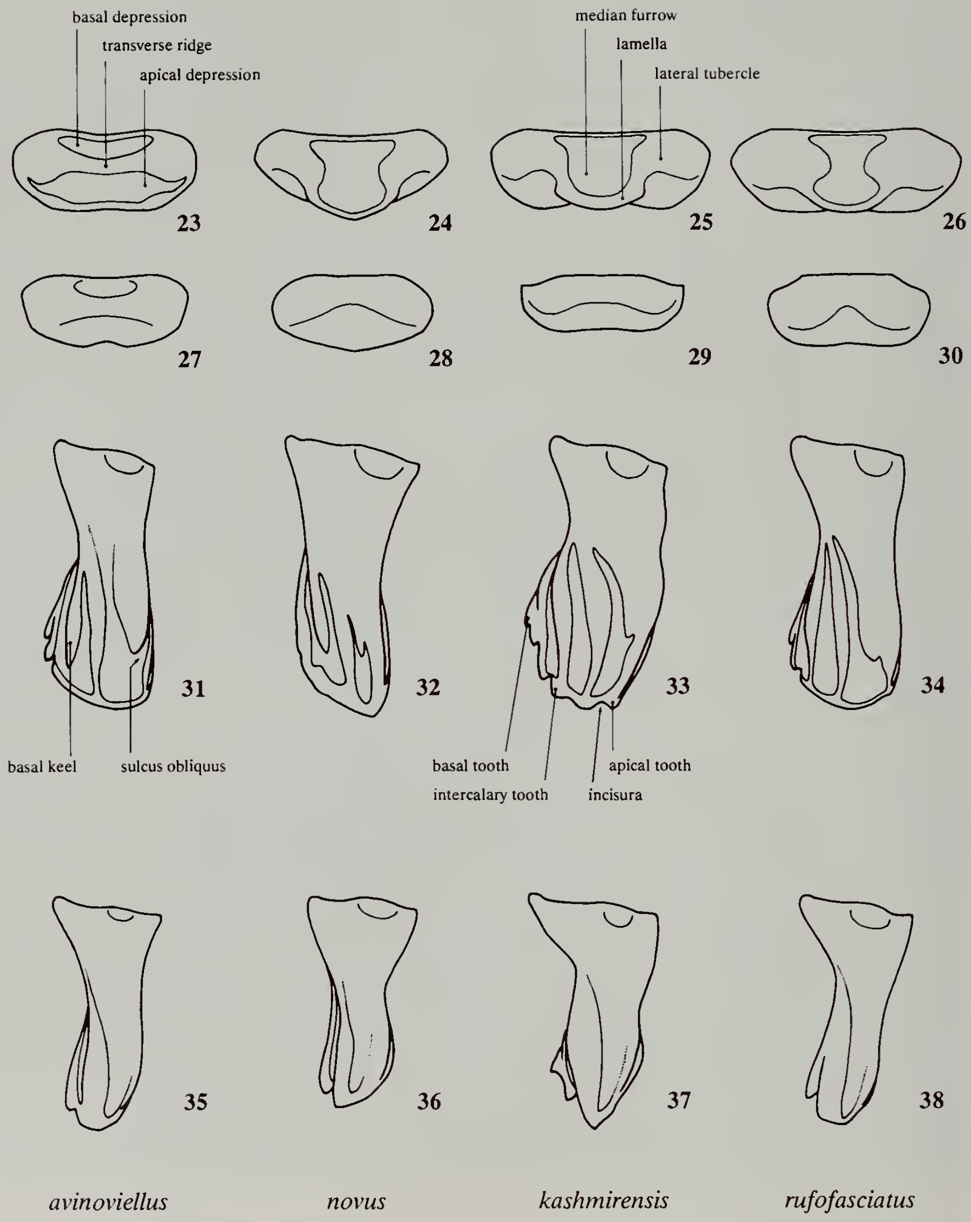
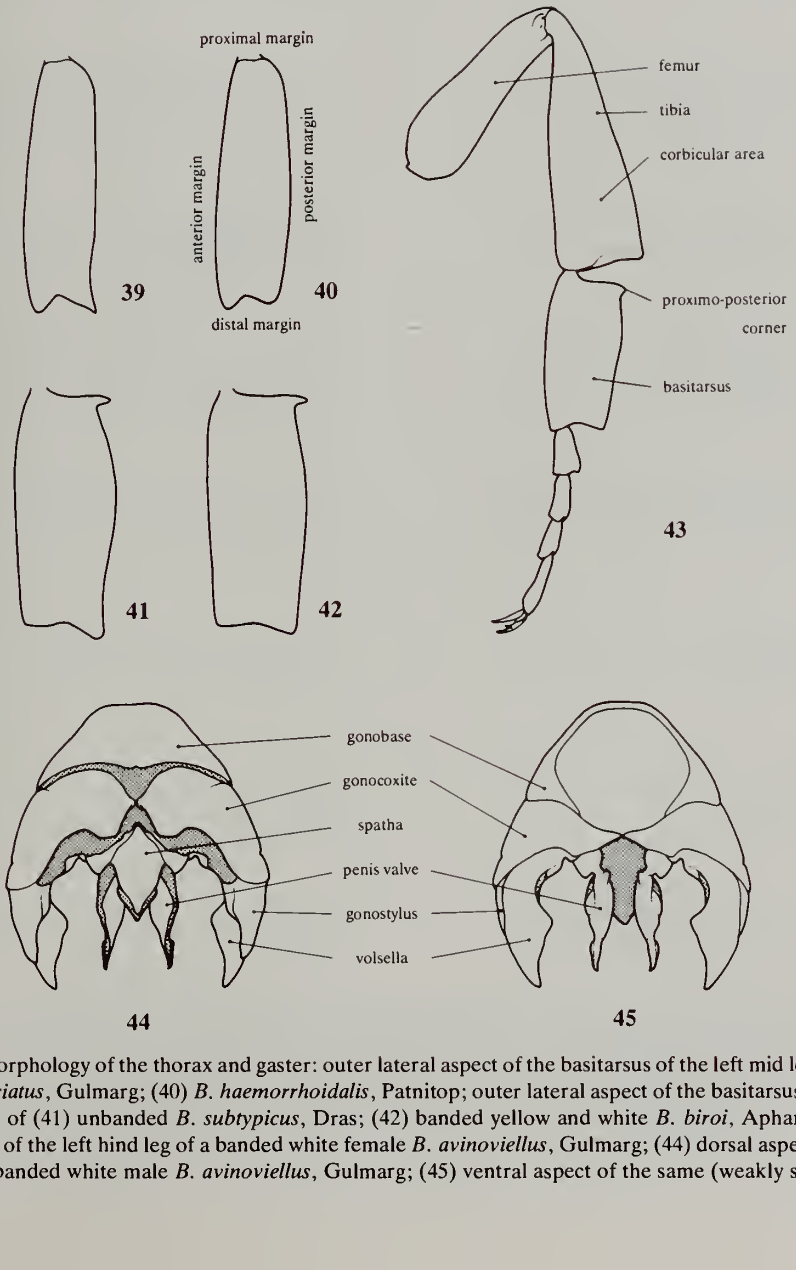
Plate 1 Representatives of the *rufofasciatus*-group from the Vale of Kashmir. In this part of their distribution, all three species show caste-dependent colour dimorphism among females. There is also gender-dependent colour variation among *Bombus pyrosoma* and *B. simillimus*. Top row: *B. rufofasciatus* (left to right: queen, worker, male), from a nest on Mt Apharwat, in subalpine pasture. Middle row: *B. Pyrosoma* (queen, worker, male), from a nest on Apharwat, in the coniferous forest. Bottom row: *B. simillimus* (queen, worker, male), from a nest near Harwan, in valley scrub. Photographed by Harry Taylor, BMNH photographic unit.



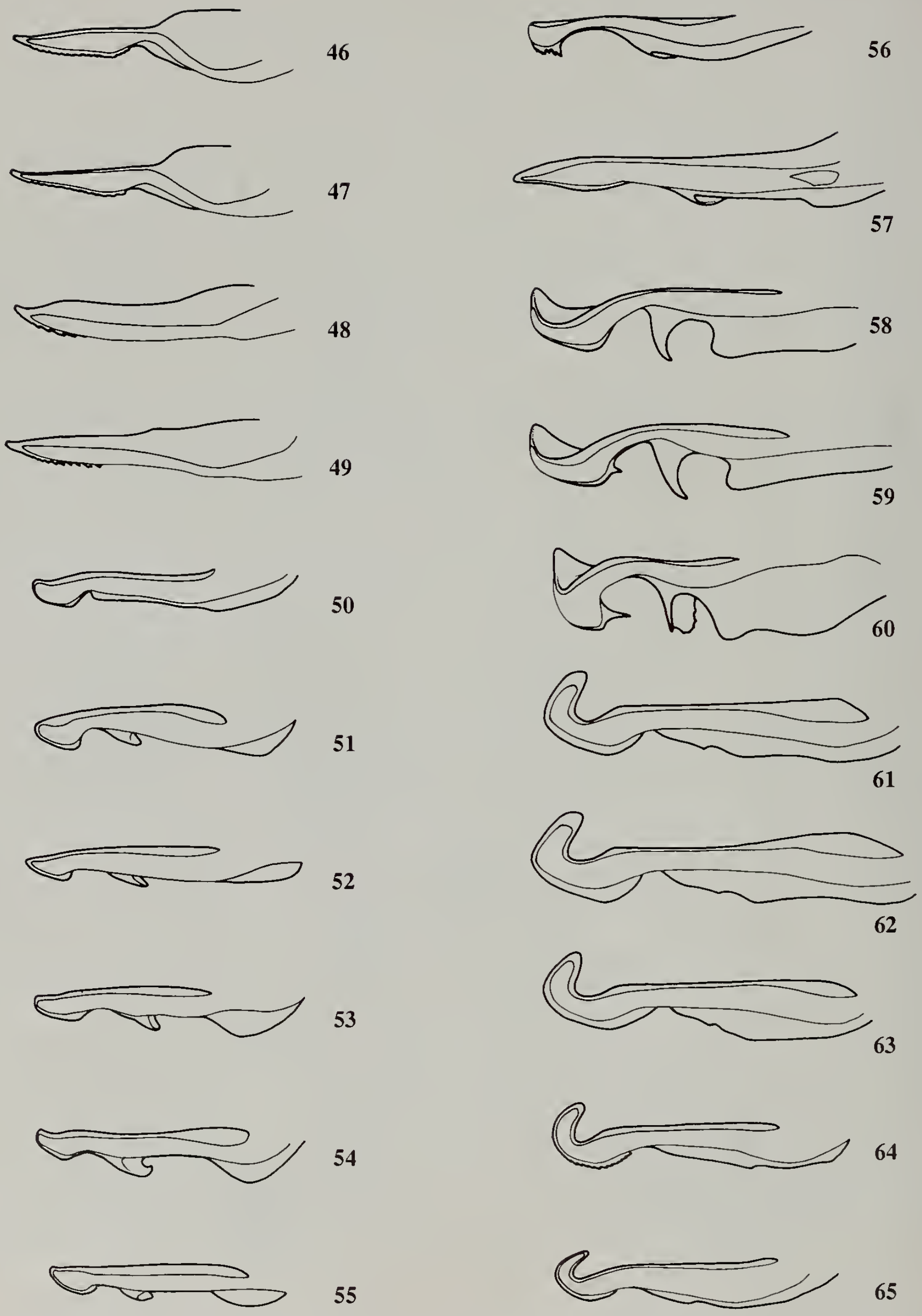
Figs 14–22 Morphology of the head: (14) anterior aspect of the head of a banded white queen *B. avinoviellus*, Gulmarg; (15) left lateral aspect of a worker *B. lemniscatus*, Apharwat, showing measurements of the malar area; (16) dorsal aspect of a banded white queen *B. avinoviellus*, Gulmarg, showing measurements of the ocello-ocular area; dorsal aspect of segments 3–5 of the left antenna of queens of (17) *B. trifasciatus*, Gulmarg; (18) *B. haemorrhoidalis*, Muzaffarabad; (19) banded white *B. asiaticus*, Gulmarg; (20) *B. oberti*, Nimaling; the same, males of (21) *B. bohemicus*, Lal Pani; (22) *B. ferganicus*, Gulmarg.



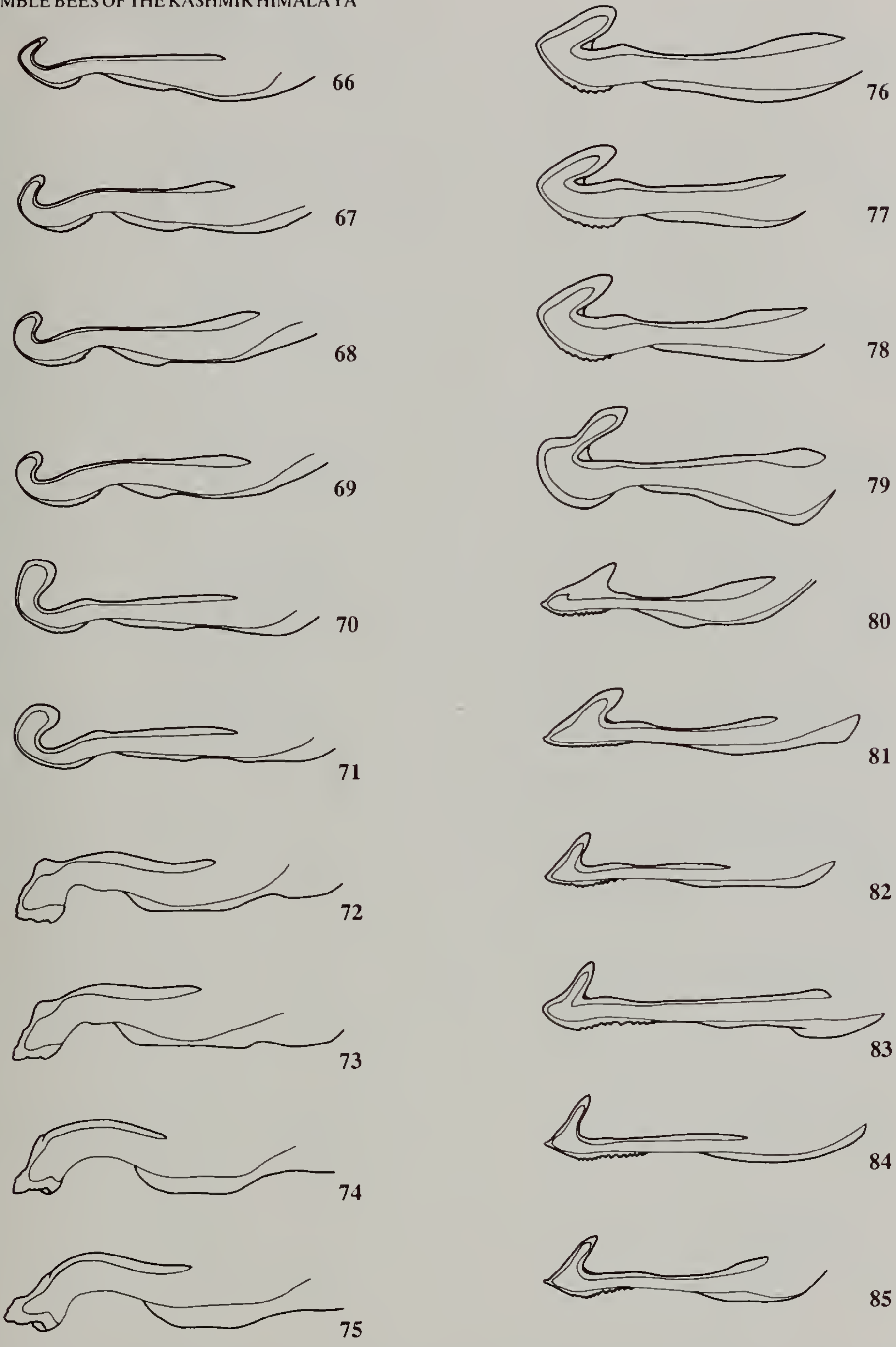
Figs 23–38 Morphology of the head: anterior aspect of the labrum of females of (23) banded white *B. avinoviellus*, Gulmarg; (24) *B. novus*, Apharwat; (25) yellow and white *B. kashmirensis*, Apharwat; (26) *B. rufofasciatus*, Apharwat; anterior aspect of the labrum of males of (27) banded white *B. avinoviellus*, Gulmarg; (28) *B. novus*, Apharwat; (29) yellow and white *B. kashmirensis*, Apharwat; (30) *B. rufofasciatus*, Apharwat; outer lateral aspect of the left mandible of females of (31) banded white *B. avinoviellus*, Gulmarg; (32) *B. novus*, Apharwat; (33) yellow and white *B. kashmirensis*, Apharwat; (34) *B. rufofasciatus*, Apharwat; outer lateral aspect of the left mandible of males of (35) banded white *B. avinoviellus*, Gulmarg; (36) *B. novus*, Apharwat; (37) yellow and white *B. kashmirensis*, Apharwat; (38) *B. rufofasciatus*, Apharwat.



Figs 39–45 Morphology of the thorax and gaster: outer lateral aspect of the basitarsus of the left mid leg of workers of (39) *B. trifasciatus*, Gulmarg; (40) *B. haemorrhoidalis*, Patnitop; outer lateral aspect of the basitarsus of the left hind leg of queens of (41) unbanded *B. subtypicus*, Dras; (42) banded yellow and white *B. biroi*, Apharwat; (43) outer lateral aspect of the left hind leg of a banded white female *B. avinoviellus*, Gulmarg; (44) dorsal aspect of the genital capsule of a banded white male *B. avinoviellus*, Gulmarg; (45) ventral aspect of the same (weakly sclerotised areas stippled).



Figs 46–65 Morphology of the male genitalia: postero-dorsal aspect of the right penis valve of (46) banded yellow *B. avinoviellus*, Lal Pani; (47) banded white *B. avinoviellus*, Gulmarg; (48) yellow and white *B. himalayanus*, Apharwat; (49) *B. marussinus*, Batakush; (50) *B. bohemicus*, Lal Pani; (51) *B. novus*, Apharwat; (52) *B. branickii*, Chogdo; (53) *B. ferganicus*, Gulmarg; (54) yellow *B. morawitzianus*, Batakush; (55) *B. skorikovi*, Lal Pani; (56) *B. trifasciatus*, Harwan; (57) *B. haemorrhoidalis*, Muzaffarabad; (58) unbanded *B. melanurus*, Chogdo; (59) unbanded *B. melanurus*, Gulmarg; (60) *B. personatus*, Chogdo; (61) yellow *B. kashmirensis*, Chogdo; (62) yellow and white *B. kashmirensis*, Apharwat; (63) white *B. kashmirensis*, Lal Pani; (64) *B. hypnorum*, Apharwat; (65) banded *B. subtypicus*, Lal Pani.



Figs 66–85 Morphology of the male genitalia: postero-dorsal aspect of the right penis valve of (66) unbanded *B. subtypicus*, Lal Pani; (67) *B. lemniscatus*, Uttar Pradesh; (68) *B. lepidus* [with yellow females], Dalti; (69) *B. lepidus* [with yellow and white females], Nigagar; (70) unbanded *B. biroi*, Suru; (71) banded *B. biroi*, Apharwat; (72) dark *B. tunicatus*, Shigar; (73) light *B. tunicatus*, Gulmarg; (74) dark *B. lucorum*, Gilgit; (75) light *B. lucorum*, Apharwat; (76) unbanded yellow [red-tailed] *B. asiaticus*, Leh; (77) banded yellow black-tailed *B. asiaticus*, Nigagar; (78) banded white [red-tailed] *B. asiaticus*, Gulmarg; (79) *B. oberti*, Pamir; (80) *B. ladakhensis*, Hemis; (81) *B. semenovianus*, Hemis; (82) *B. keriensis* [with yellow females], Apharwat; (83) *B. simillimus*, Banihal; (84) *B. pyrosoma*, Apharwat; (85) *B. rufofasciatus*, Apharwat.

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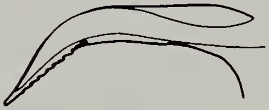

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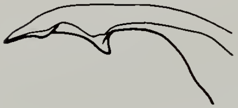

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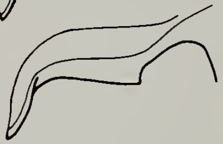

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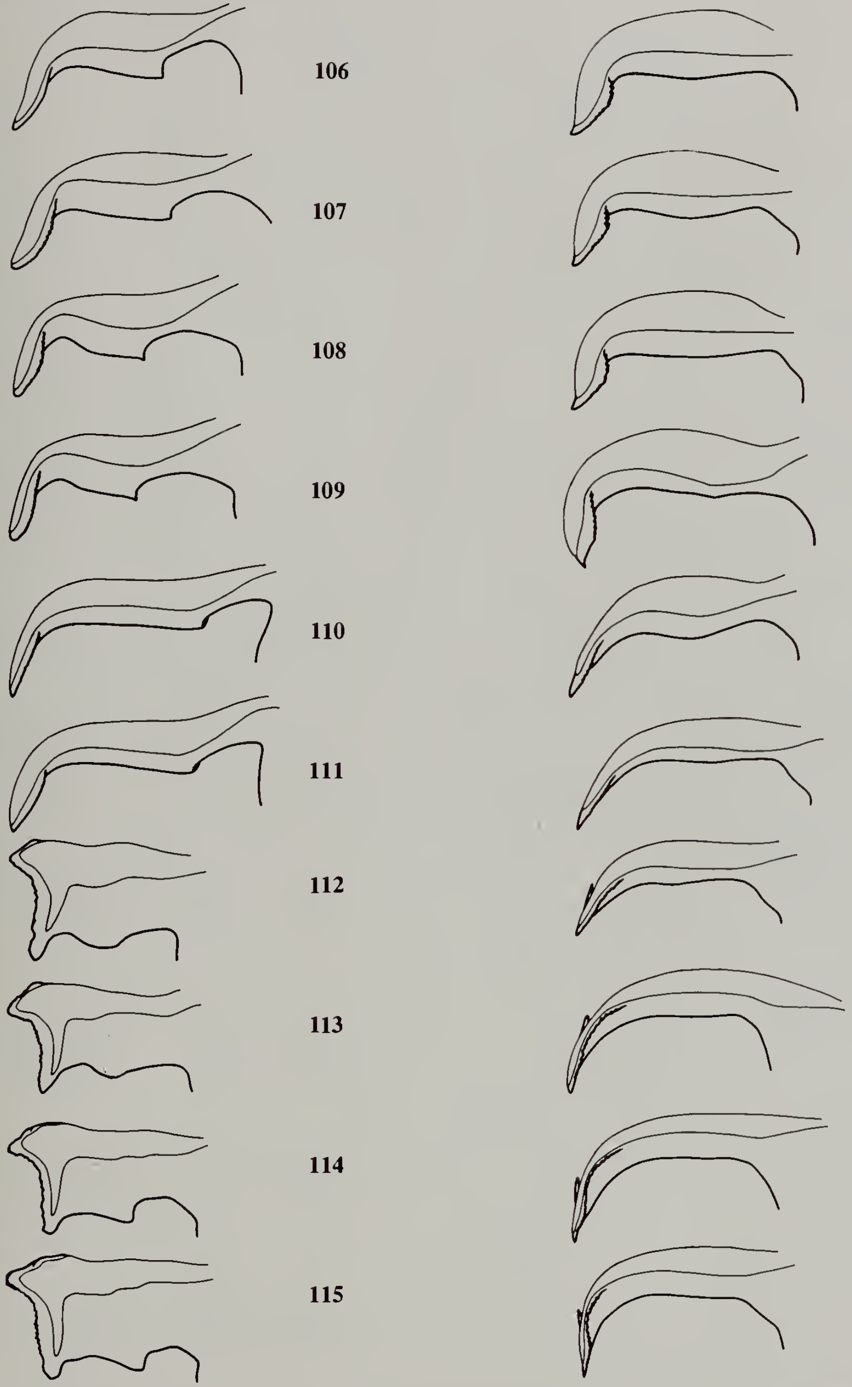
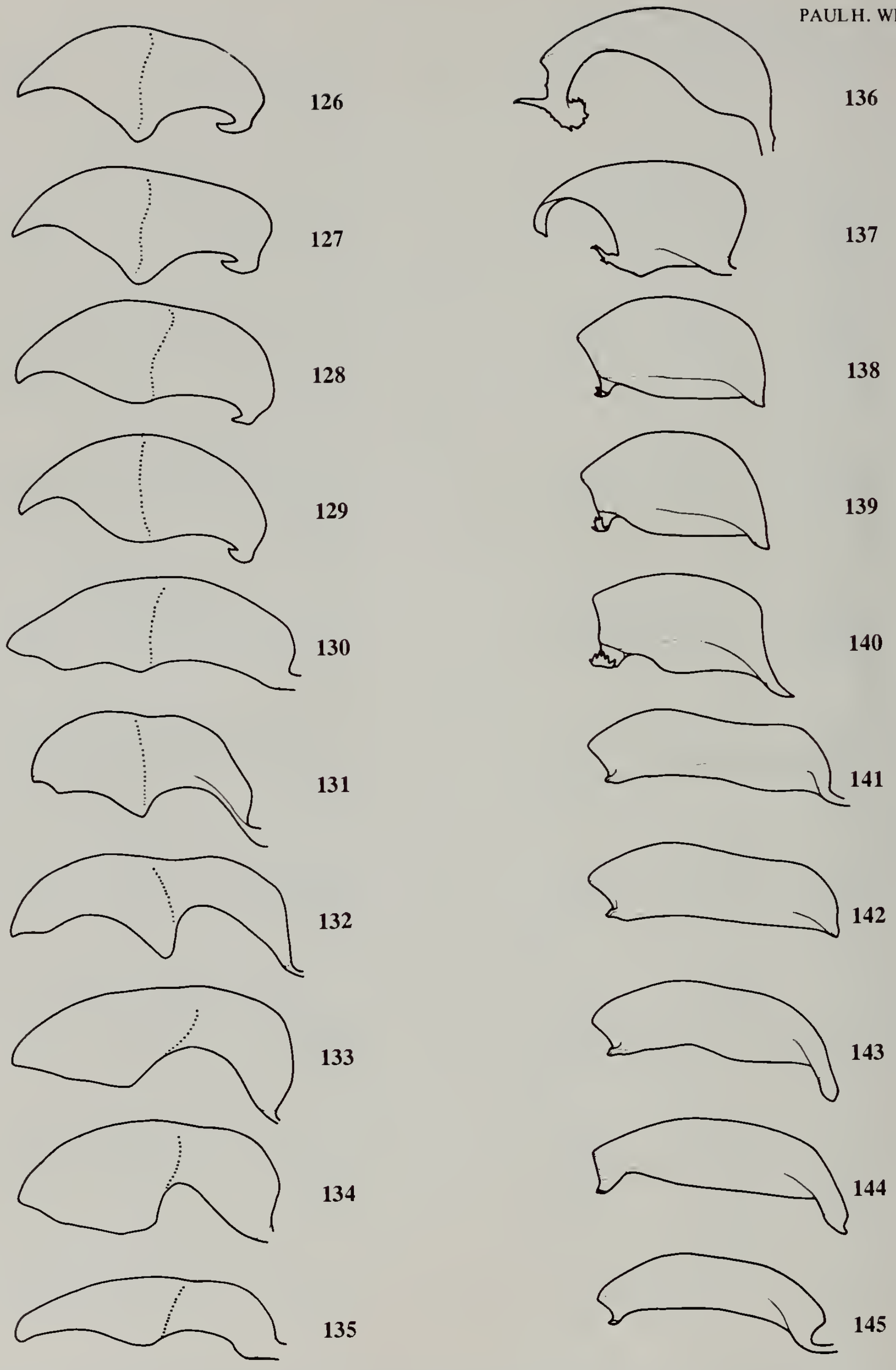
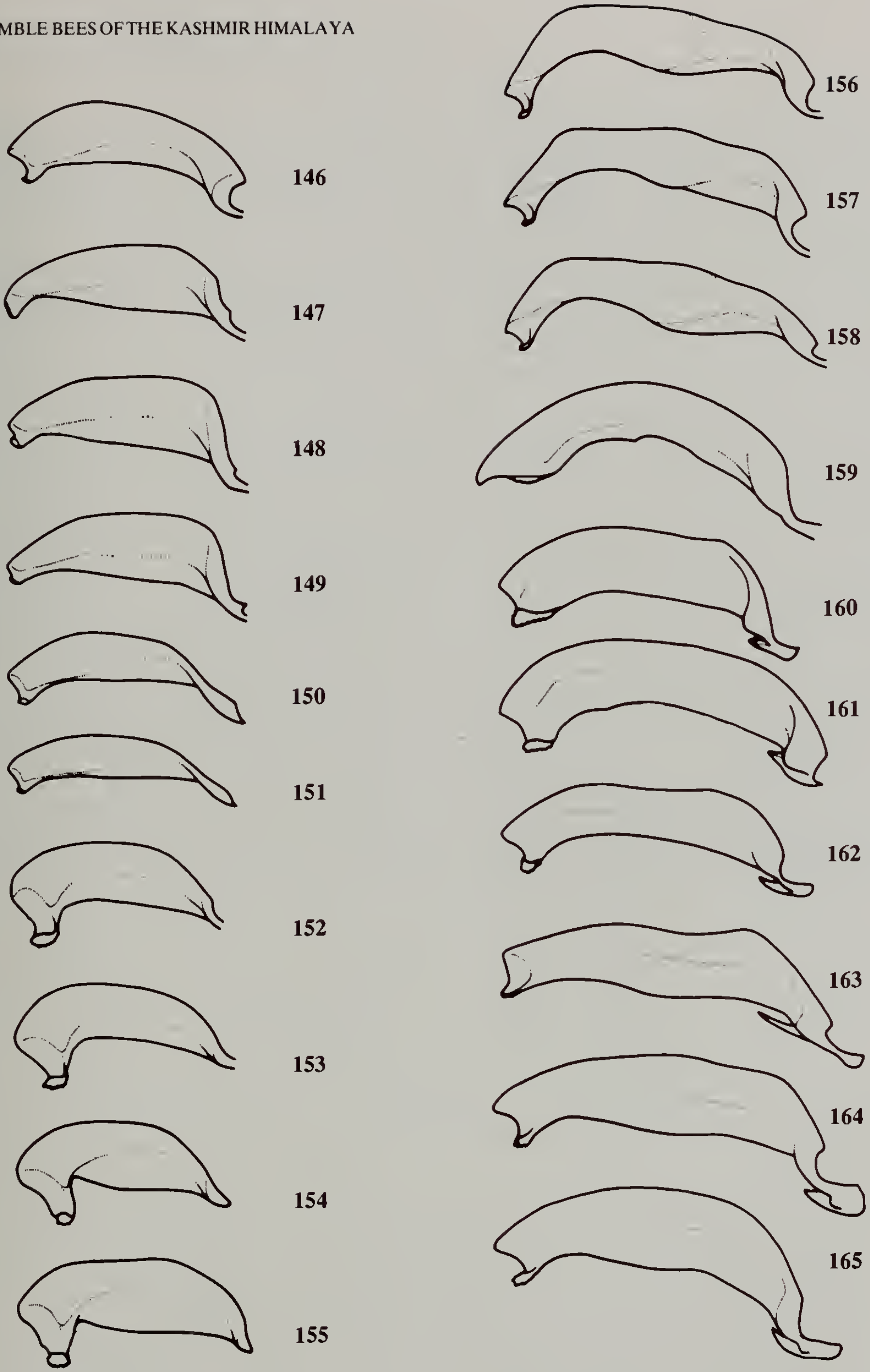
Figs 86–105 Morphology of the male genitalia: outer lateral aspect of the right penis valve of (86) banded yellow *B. avinoviellus*, Lal Pani; (87) banded white *B. avinoviellus*, Gulmarg; (88) yellow and white *B. himalayanus*, Apharwat; (89) *B. marussinus*, Batakush; (90) *B. bohemicus*, Lal Pani; (91) *B. novus*, Apharwat; (92) *B. branickii*, Chogdo; (93) *B. ferganicus*, Gulmarg; (94) yellow *B. morawitzianus*, Batakush; (95) *B. skorikovi*, Lal Pani; (96) *B. trifasciatus*, Harwan; (97) *B. haemorrhoidalis*, Muzaffarabad; (98) unbanded *B. melanurus*, Chogdo; (99) unbanded *B. melanurus*, Gulmarg; (100) *B. personatus*, Chogdo; (101) yellow *B. kashmirensis*, Chogdo; (102) yellow and white *B. kashmirensis*, Apharwat; (103) white *B. kashmirensis*, Lal Pani; (104) *B. hypnorum*, Apharwat; (105) banded *B. subtypicus*, Lal Pani.



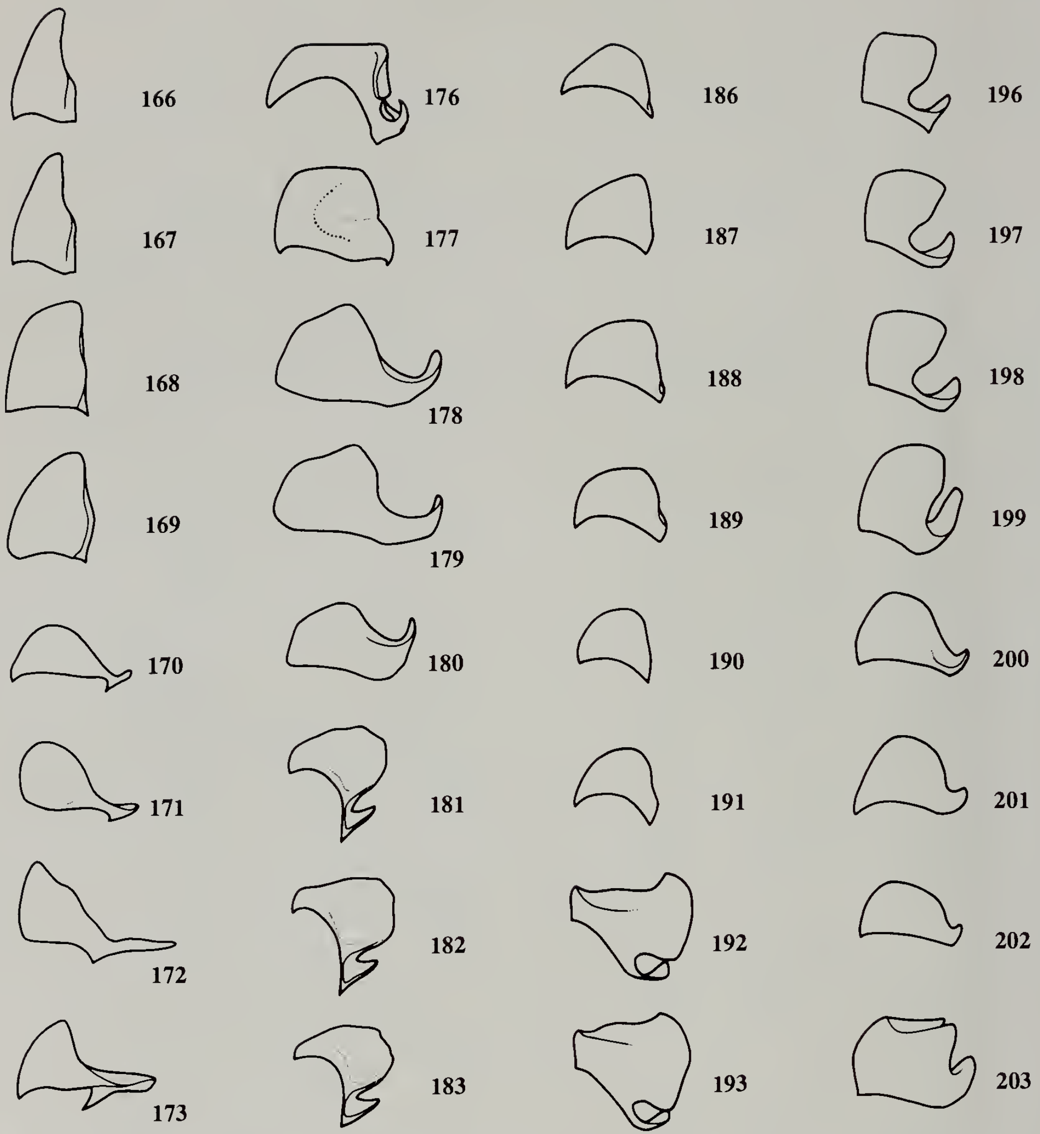
Figs 106–125 Morphology of the male genitalia: outer lateral aspect of the right penis valve of (106) unbanded *B. subtypicus*, Lal Pani; (107) *B. lemniscatus*, Uttar Pradesh; (108) *B. lepidu* [with yellow females], Dalti; (109) *B. lepidus* [with yellow and white females], Nigagar; (110) unbanded *B. biroi*, Suru; (111) banded *B. biroi*, Apharwat; (112) dark *B. tunicatus*, Shigar; (113) light *B. tunicatus*, Gulmarg; (114) dark *B. lucorum*, Gilgit; (115) light *B. lucorum*, Apharwat; (116) unbanded yellow [red-tailed] *B. asiaticus*, Leh; (117) banded yellow black-tailed *B. asiaticus*, Nigagar; (118) banded white [red-tailed] *B. asiaticus*, Gulmarg; (119) *B. oberti*, Pamir; (120) *B. ladakhensis*, Hemis; (121) *B. semenovianus*, Hemis; (122) *B. keriensis* [with yellow females], Apharwat; (123) *B. simillimus*, Banihal; (124) *B. pyrosoma*, Apharwat; (125) *B. rufofasciatus*, Apharwat.



Figs 126–145 Morphology of the male genitalia: interio-ventral aspect of the right volsella of (126) banded yellow *B. avinoviellus*, Lal Pani; (127) banded white *B. avinoviellus*, Gulmarg; (128) yellow and white *B. himalayanus*, Apharwat; (129) *B. marussinus*, Batakush; (130) *B. bohemicus*, Lal Pani; (131) *B. novus*, Apharwat; (132) *B. branickii*, Chogdo; (133) *B. ferganicus*, Gulmarg; (134) yellow *B. morawitzianus*, Batakush; (135) *B. skorikovi*, Lal Pani; (136) *B. trifasciatus*, Harwan; (137) *B. haemorrhoidalis*, Muzaffarabad; (138) unbanded *B. melanurus*, Chogdo; (139) unbanded *B. melanurus*, Gulmarg; (140) *B. personatus*, Chogdo; (141) yellow *B. kashmirensis*, Chogdo; (142) yellow and white *B. kashmirensis*, Apharwat; (143) white *B. kashmirensis*, Lal Pani; (144) *B. hypnorum*, Apharwat; (145) banded *B. subtypicus*, Lal Pani.



Figs 146–165 Morphology of the male genitalia: interio-ventral aspect of the right volsella of (146) unbanded *B. subtypicus*, Lal Pani; (147) *B. lemniscatus*, Uttar Pradesh; (148) *B. lepidus* [with yellow females], Dalti; (149) *B. lepidus* [with yellow and white females], Nigagar; (150) unbanded *B. biroi*, Suru; (151) banded *B. biroi*, Apharwat; (152) dark *B. tunicatus*, Shigar; (153) light *B. tunicatus*, Gulmarg; (154) dark *B. lucorum*, Gilgit; (155) light *B. lucorum*, Apharwat; (156) unbanded yellow [red-tailed] *B. asiaticus*, Leh; (157) banded yellow black-tailed *B. asiaticus*, Nigagar; (158) banded white [red-tailed] *B. asiaticus*, Gulmarg; (159) *B. oberti*, Pamir; (160) *B. ladakhensis*, Hemis; (161) *B. semenovianus*, Hemis; (162) *B. keriensis* [with yellow females], Apharwat; (163) *B. simillimus*, Banihal; (164) *B. pyrosoma*, Apharwat; (165) *B. rufofasciatus*, Apharwat.



Figs 166–205 Morphology of the male genitalia: dorsal aspect of the right gonostylus of (166) banded yellow *B. avinoviellus*, Lal Pani; (167) banded white *B. avinoviellus*, Gulmarg; (168) yellow and white *B. himalayanus*, Apharwat; (169) *B. marussinus*, Batakush; (170) *B. bohemicus*, Lal Pani; (171) *B. novus*, Apharwat; (172) *B. branickii*, Chogdo; (173) *B. ferganicus*, Gulmarg; (174) yellow *B. morawitzianus*, Batakush; (175) *B. skorikovi*, Lal Pani; (176) *B. trifasciatus*, Harwan; (177) *B. haemorrhoidalis*, Muzaffarabad; (178) unbanded *B. melanurus*, Chogdo; (179) unbanded *B. melanurus*, Gulmarg; (180) *B. personatus*, Chogdo; (181) yellow *B. kashmirensis*, Chogdo; (182) yellow and white *B. kashmirensis*, Apharwat; (183) white *B. kashmirensis*, Lal Pani; (184) *B. hypnorum*, Apharwat; (185) banded *B. subtypicus*, Lal Pani; (186) unbanded *B. subtypicus*, Lal Pani; (187) *B. lemniscatus*, Uttar Pradesh; (188) *B. lepidus* [with yellow females], Dalti; (189) *B. lepidus* [with yellow and white females], Nigagar; (190) unbanded *B. biroi*, Suru; (191) banded *B. biroi*, Apharwat; (192) dark *B. tunicatus*, Shigar; (193) light *B. tunicatus*, Gulmarg; (194) dark *B. lucorum*, Gilgit; (195) light *B. lucorum*, Apharwat; (196) unbanded yellow [red-tailed] *B. asiaticus*, Leh; (197) banded yellow black-tailed *B. asiaticus*, Nigagar; (198) banded white [red-tailed] *B. asiaticus*, Gulmarg; (199) *B. oberti*, Pamir; (200) *B. ladakhensis*, Hemis; (201) *B. semenovianus*, Hemis; (202) *B. keriensis* [with yellow females], Apharwat; (203) *B. simillimus*, Banihal; (204) *B. pyrosoma*, Apharwat; (205) *B. rufofasciatus*, Apharwat.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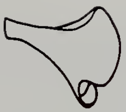
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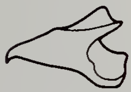
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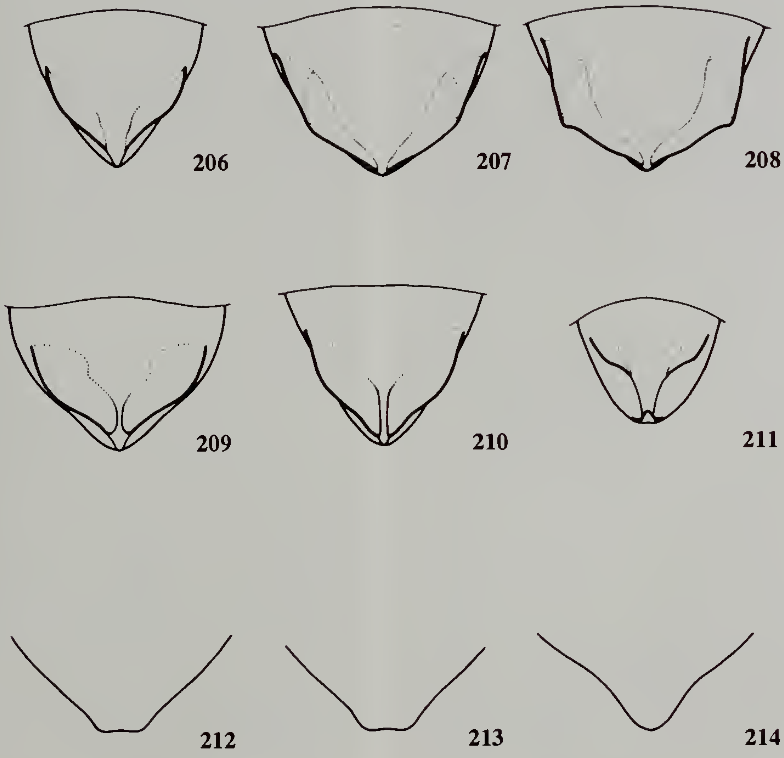
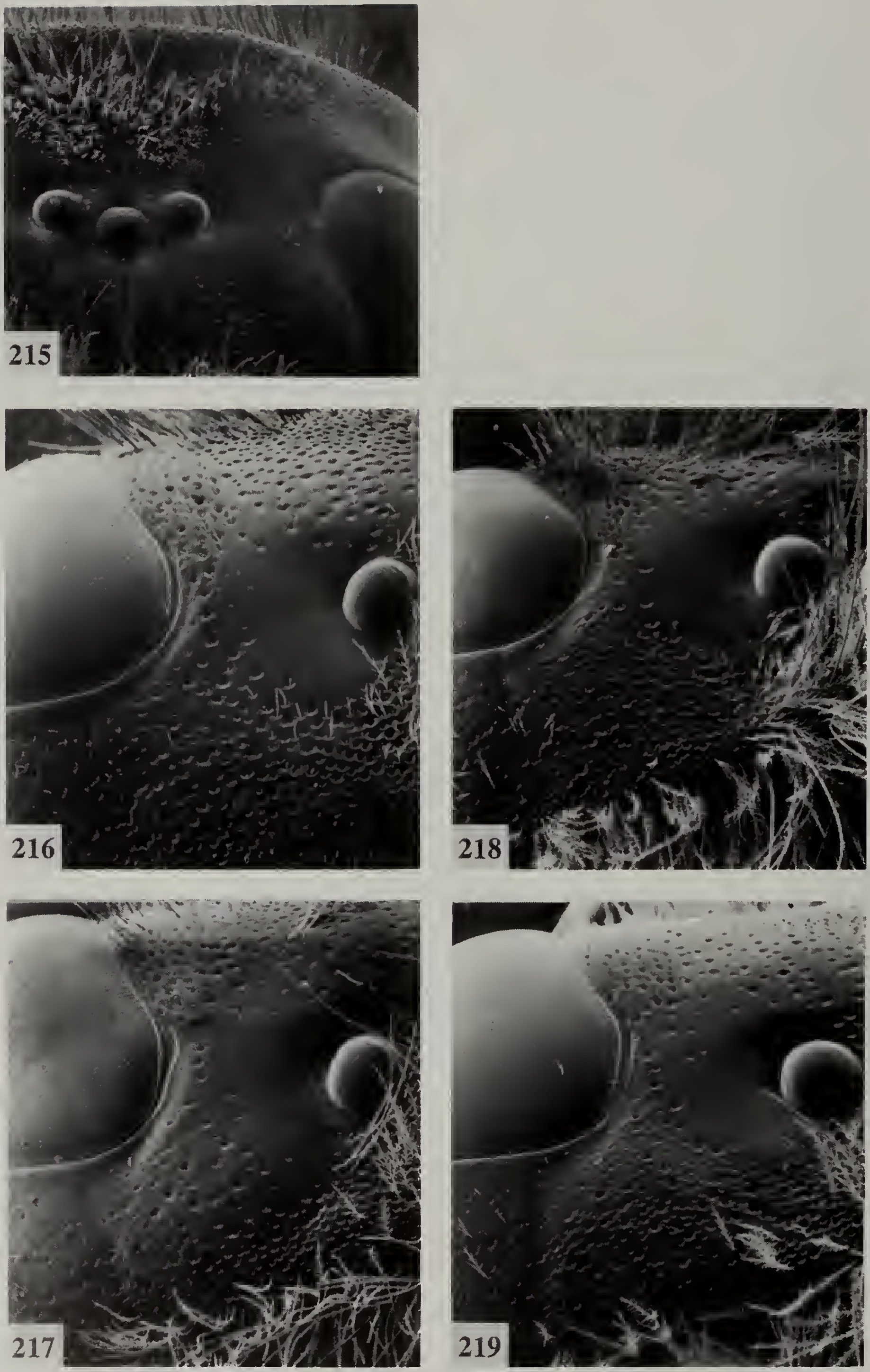
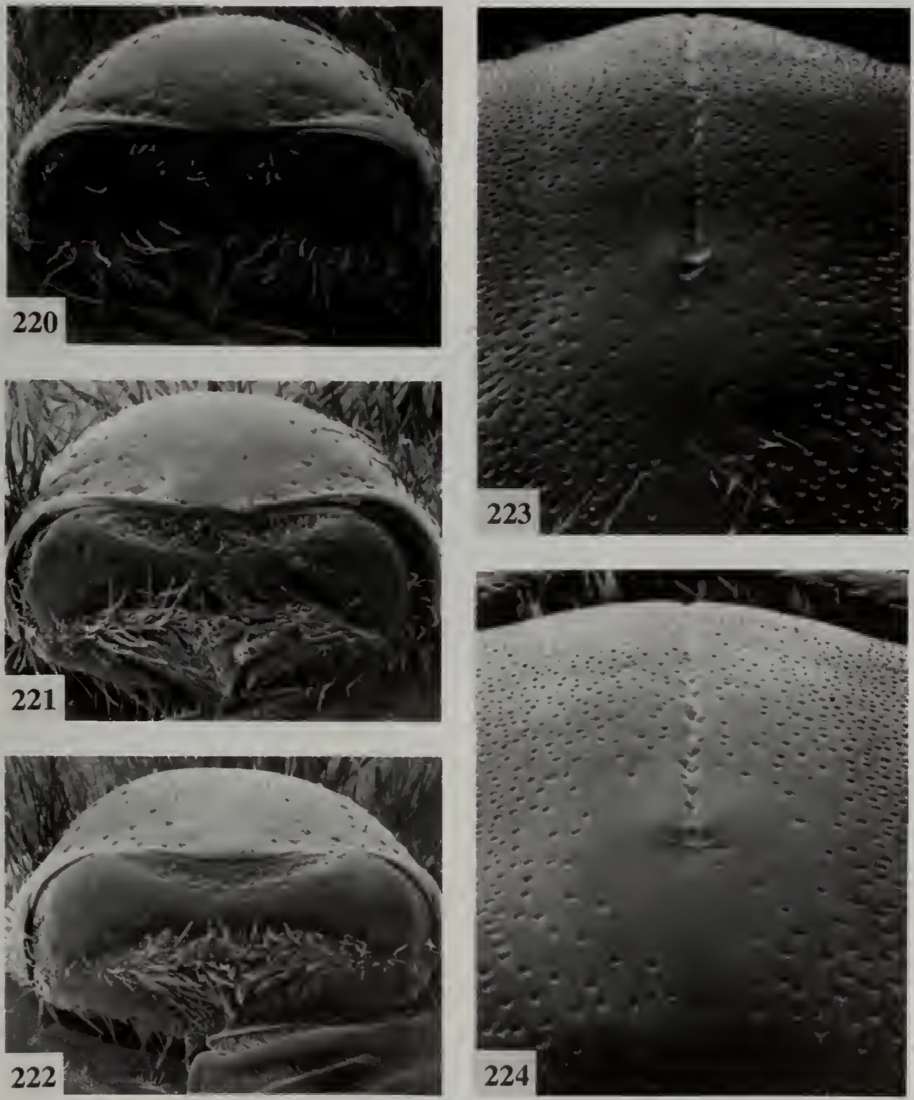


Figs 206–214 Morphology of the gaster: ventral aspect of gastral sternum VI of females of (206) *B. bohemicus*, Britain; (207) *B. novus*, Apharwat; (208) *B. branickii*, Nimaling; (209) *B. ferganicus*, Gulmarg; (210) *B. morawitzianus*, Lal Pani; (211) *B. skorikovi*, Lal Pani; dorsal aspect of the apex of gastral tergum VI of queens of (212) *B. lemniscatus*, Nepal; (213) yellow and white *B. lepidus*, Apharwat; (214) banded yellow and white *B. biroi*, Apharwat.



Figs 215–219 Morphology of the head (scanning electron micrographs, pubescence partially removed): antero-dorsal aspect of the left ocello-ocular area of the head of a queen of (215) *B. haemorrhoidalis*, Muzaffarabad; dorsal aspect of the left ocello-ocular area of the head of queens of (216) unbanded *B. subtypicus*, Afghanistan; (217) banded yellow and white *B. biroi*, 'Krishnye' Kashmir; (218) *B. lemniscatus*, Nepal; (219) yellow and white *B. lepidus*, Apharwat.



Figs 220–224 Morphology of the head and thorax (scanning electron micrographs): antero-ventral aspect of the labrum of queens of (220) banded yellow and white *B. avinoviellus*, Gulmarg; (221) yellow and white *B. himalayanus*, Atro Sar; (222) *B. marussinus*, Chhantir Gah; postero-dorsal aspect of the middle of the scutum, pubescence removed, of queens of (223) *B. lemniscatus*, Nepal; (224) yellow and white *B. lepidus*, Apharwat.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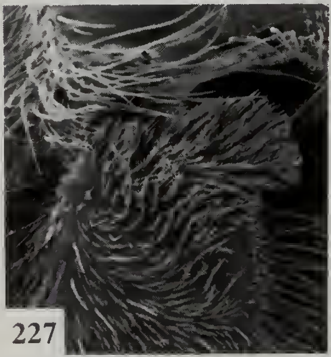
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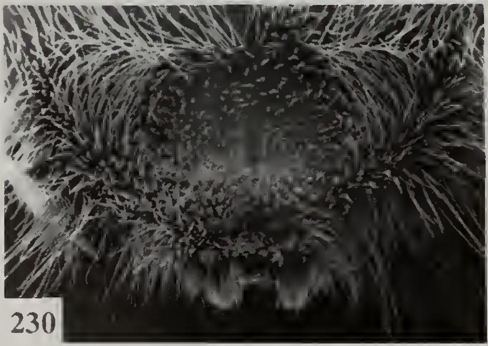
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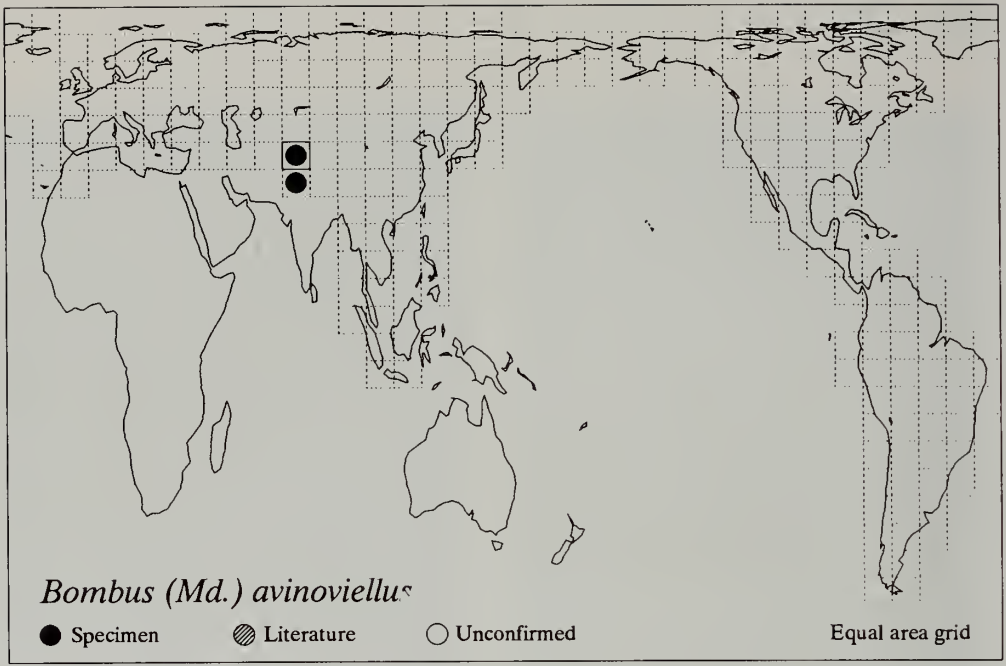
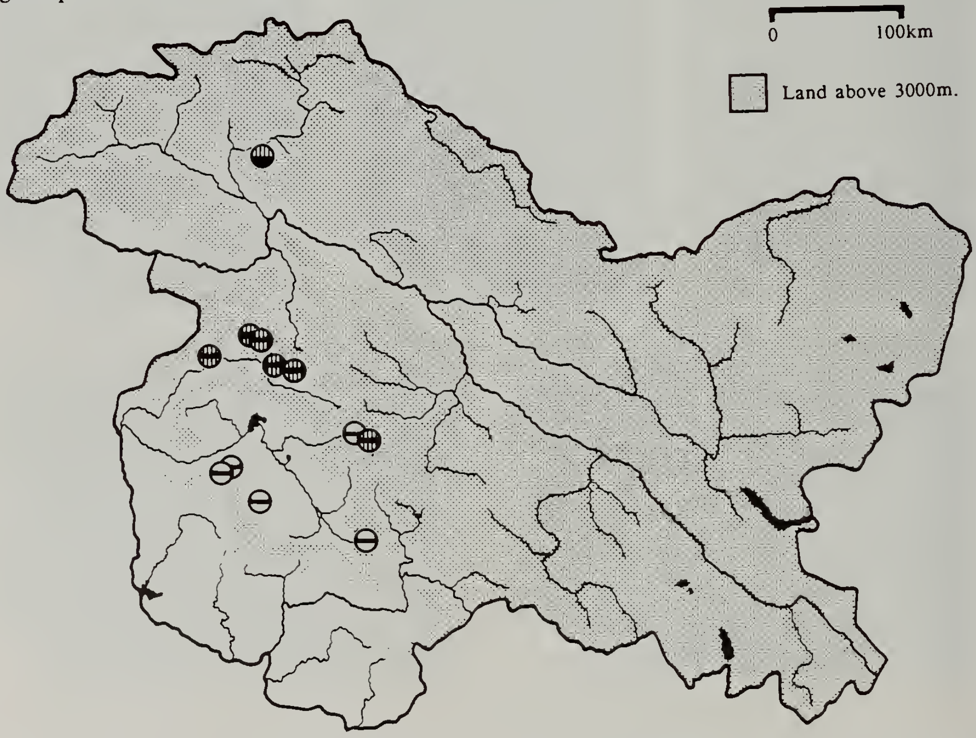
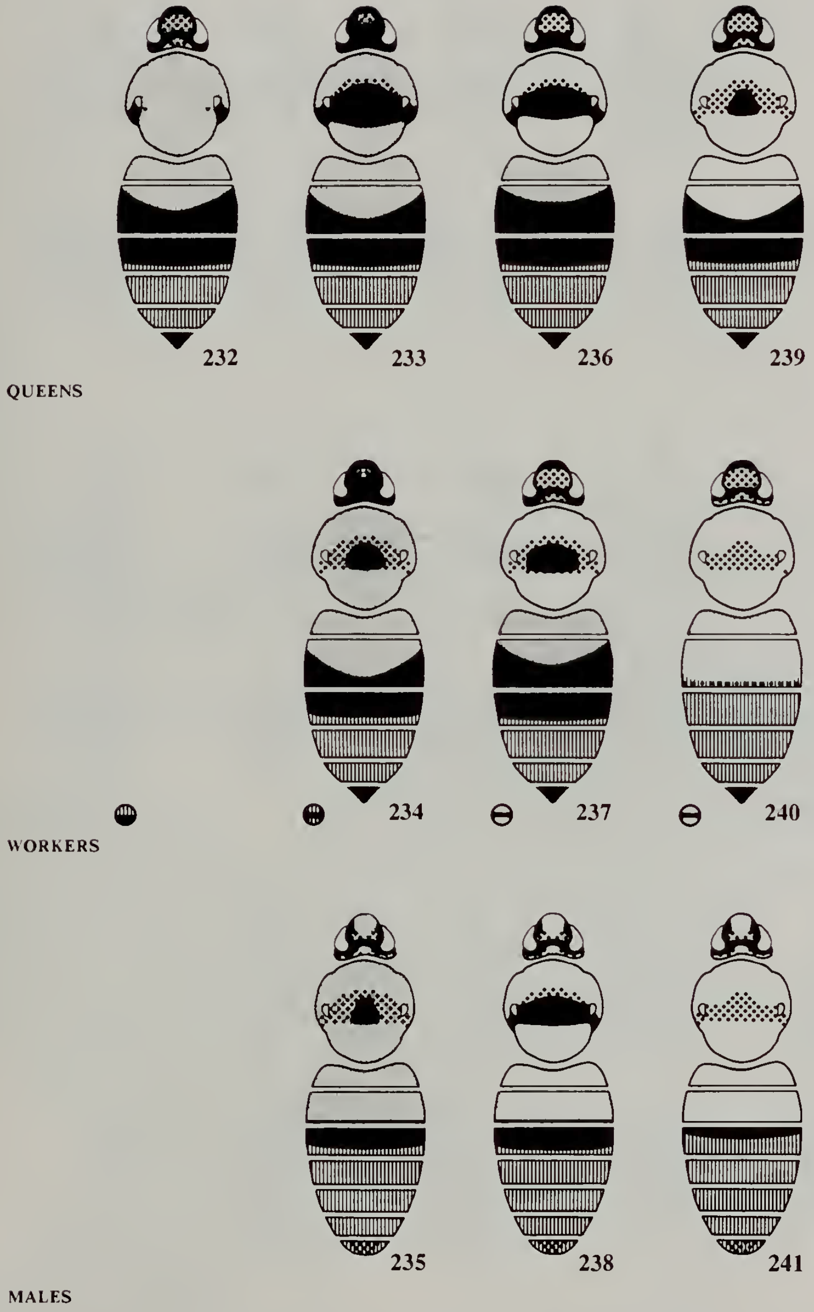
Figs 225–231 Morphology of the legs and gaster (scanning electron micrographs): outer lateral aspect of the corbicular area of the hind tibia of queens of (225) banded white *B. avinoviellus*, Gulmarg; (226) *B. simillimus*, Srinagar [the circular structures are attachment cement from the peri-anal glands of uropodid mites, det. D. Macfarlane]; outer lateral aspect of the proximo-posterior corner of the hind basitarsus of queens of (227) unbanded yellow *B. asiaticus*, Nimaling; (228) *B. oberti*, Nimaling; (229) *B. semenovianus*, Baltit; dorsal aspect of gastral tergum VI of queens of (230) *B. oberti*, Nimaling; (231) *B. semenovianus*, Baltit.



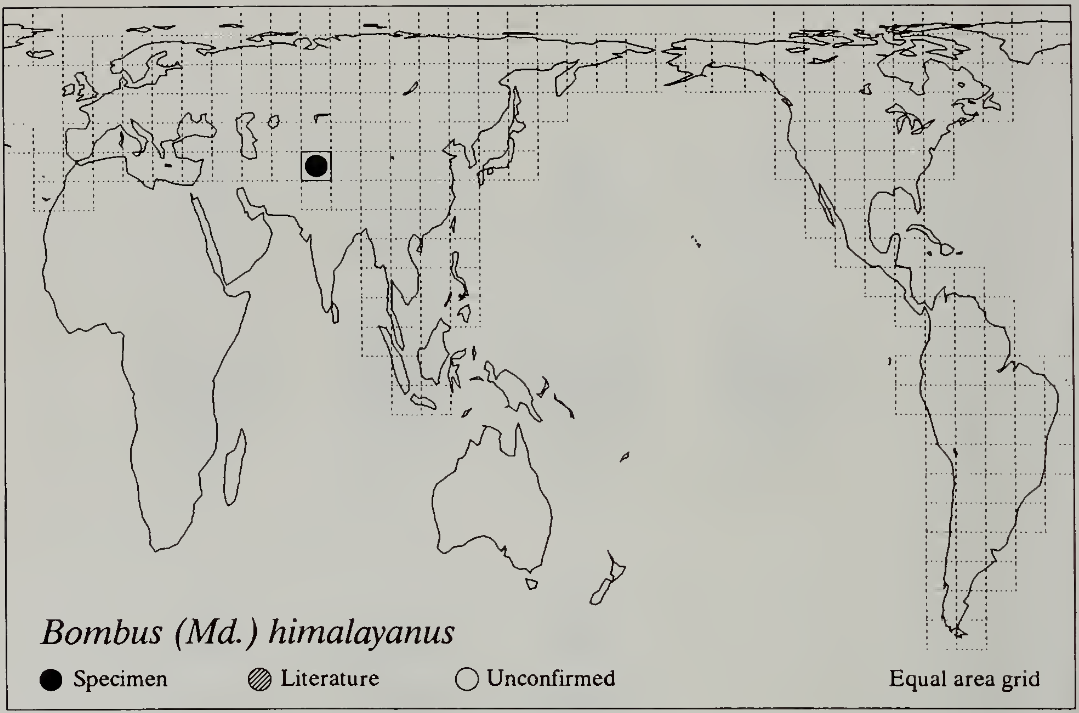
Map 5 Summary of the world-wide distribution of *B. avinoviellus* (for an explanation of the grid see Map 1). 'Specimen' records are from material examined by the author and 'Literature' records are from published data. 'Unconfirmed' records include both dubious identifications in the literature and records without precise locality data. The grid-square that includes Kashmir is shown with a solid outline.



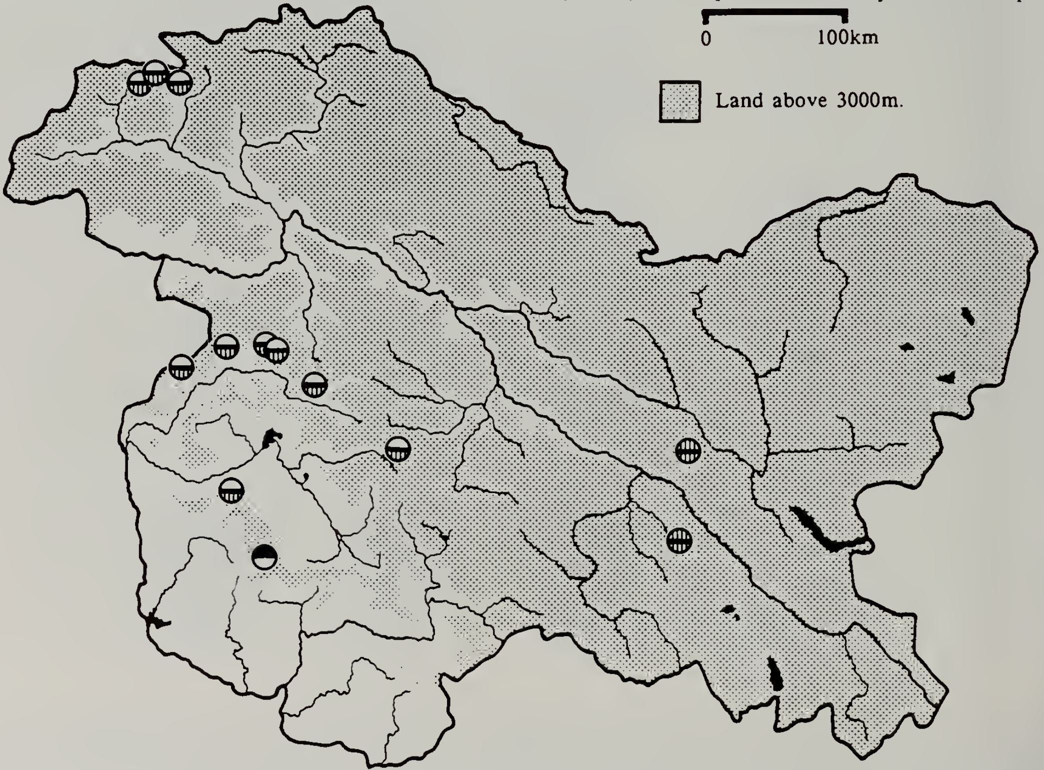
Map 6 Distribution of *B. avinoviellus* in Kashmir (for a comparison with the full range of localities sampled see Map 4). All records are from specimens that have been examined. The different symbols represent the principal colour patterns that predominate among workers in each local sample (key to colour pattern symbols see Figs 232–241).



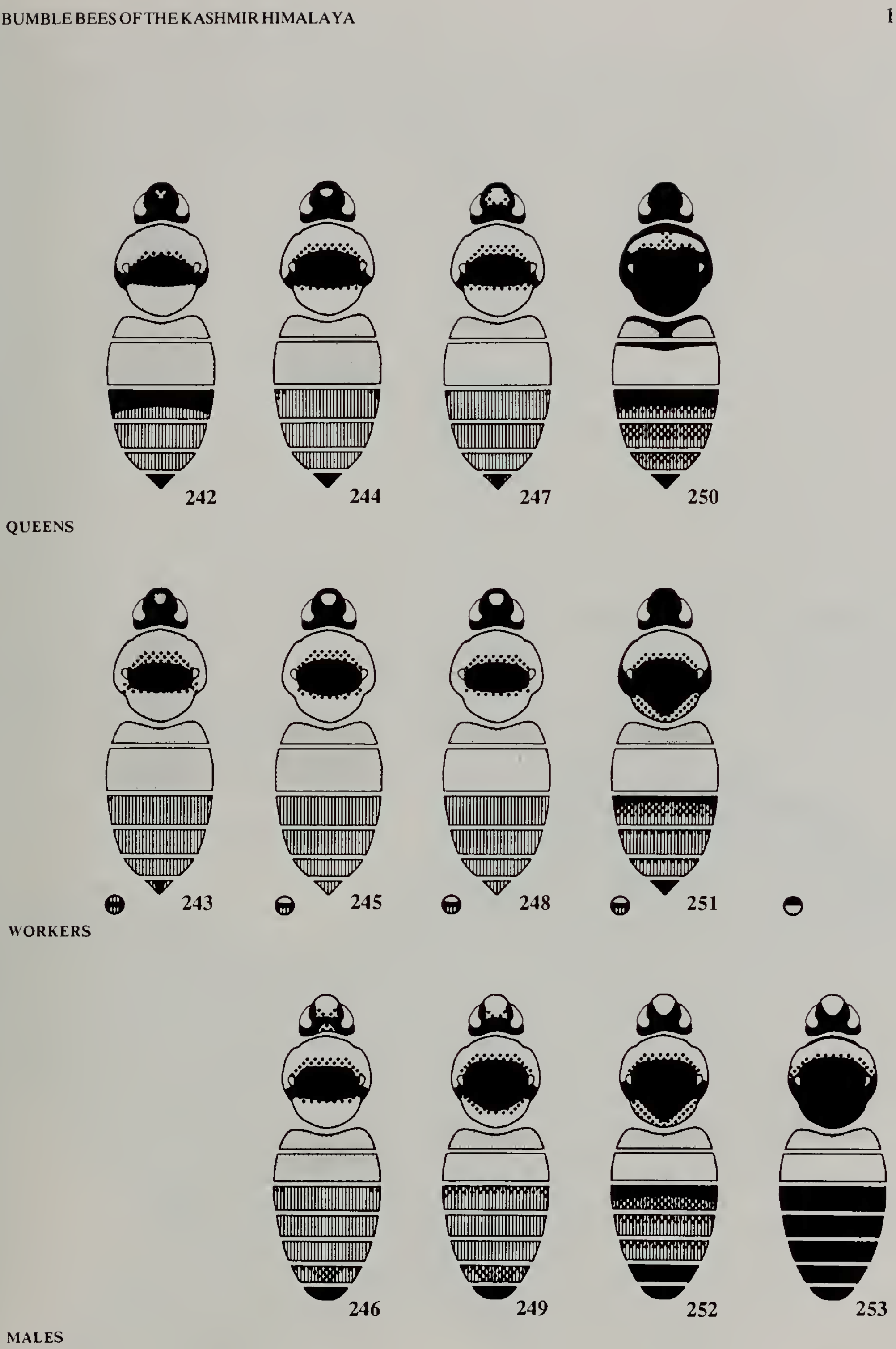
Figs 232–241 Colour patterns of *B. avinoviellus* from localities in Kashmir: (232) Banidas 30.vi–2.vii.1959, (233) Shardi 1–13.viii.1953, (234) Lal Pani 2–3.ix.1953, (235) Lal Pani 2–3.ix.1953, (236) Gulmarg vii.1986, (237) Gulmarg viii.1985, (238) Gulmarg viii.1985, (239) Gulmarg vii.1986, (240) Gulmarg viii.1985, (241) Gulmarg viii.1985 (for the colour key see Fig. 258).



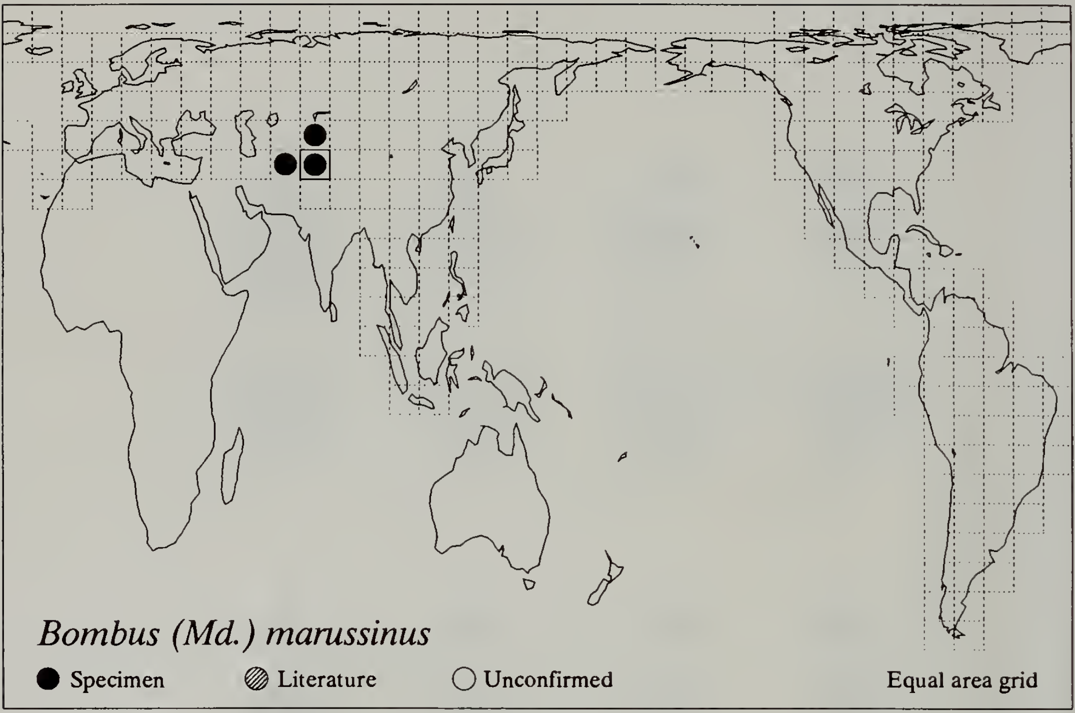
Map 7 Summary of the world-wide distribution of *B. himalayanus* (for an explanation of the symbols see Map 5).



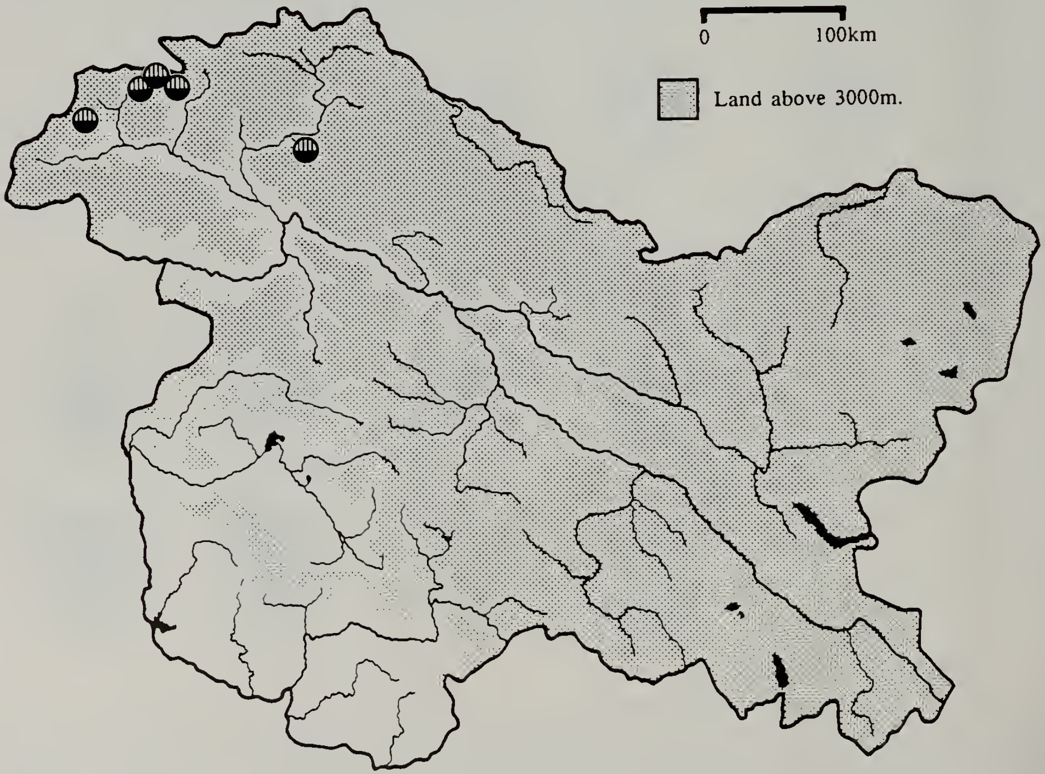
Map 8 Distribution of *B. himalayanus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 242–253).



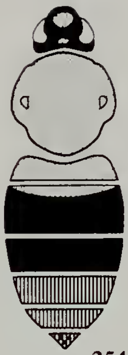
Figs 242–253 Colour patterns of *B. himalayanus* from localities in Kashmir: (242) Nimaling 17.vii.1980, (243) Chhantir Gah 5–7.viii.1954, (244) Atro Sar 11.viii.1954, (245) Atro Sar 11.viii.1954, (246) Gumri 10–11.viii.1986, (247) Atro Sar 11.viii.1954, (248) Holojut 13–14.viii.1954, (249) Apharwat 23.viii.1985, (250) Apharwat 30.viii.1985, (251) Apharwat viii.1985, (252) Apharwat 15.viii.1980, (253) Sangisfaid 1985 (for the colour key see Fig. 258).



Map 9 Summary of the world-wide distribution of *B. marussinus* (for an explanation of the symbols see Map 5).



Map 10 Distribution of *B. marussinus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 254–257).



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QUEEN

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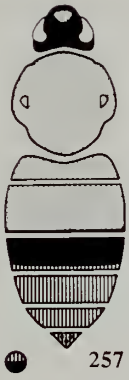

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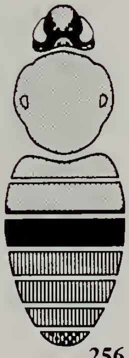
WORKERS



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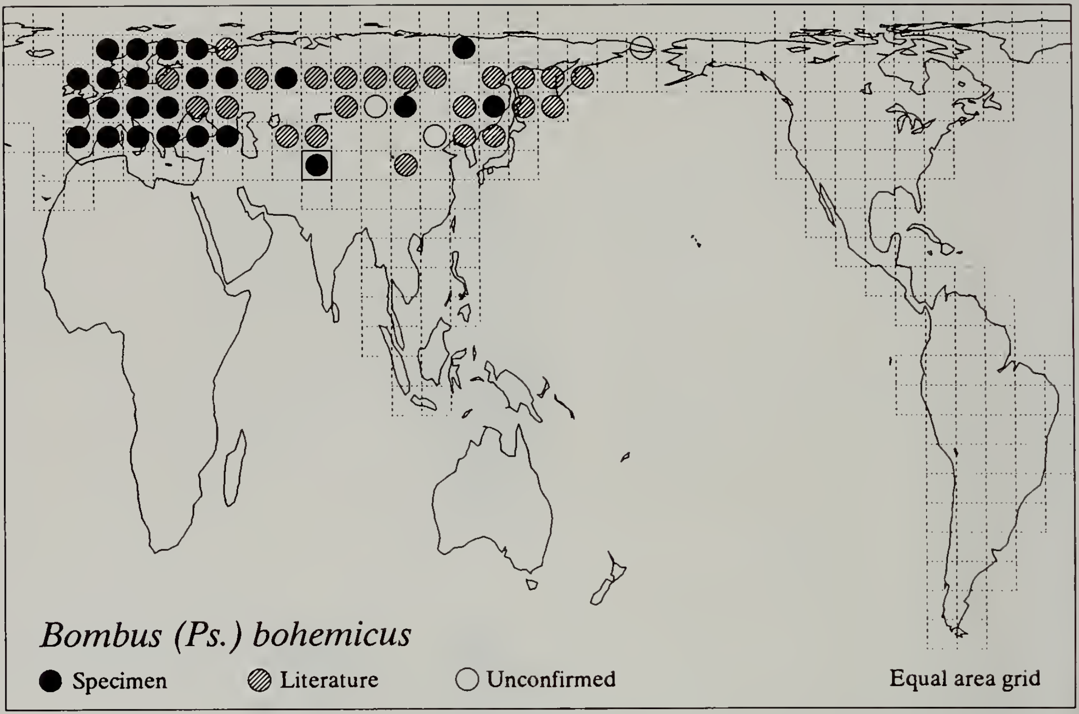
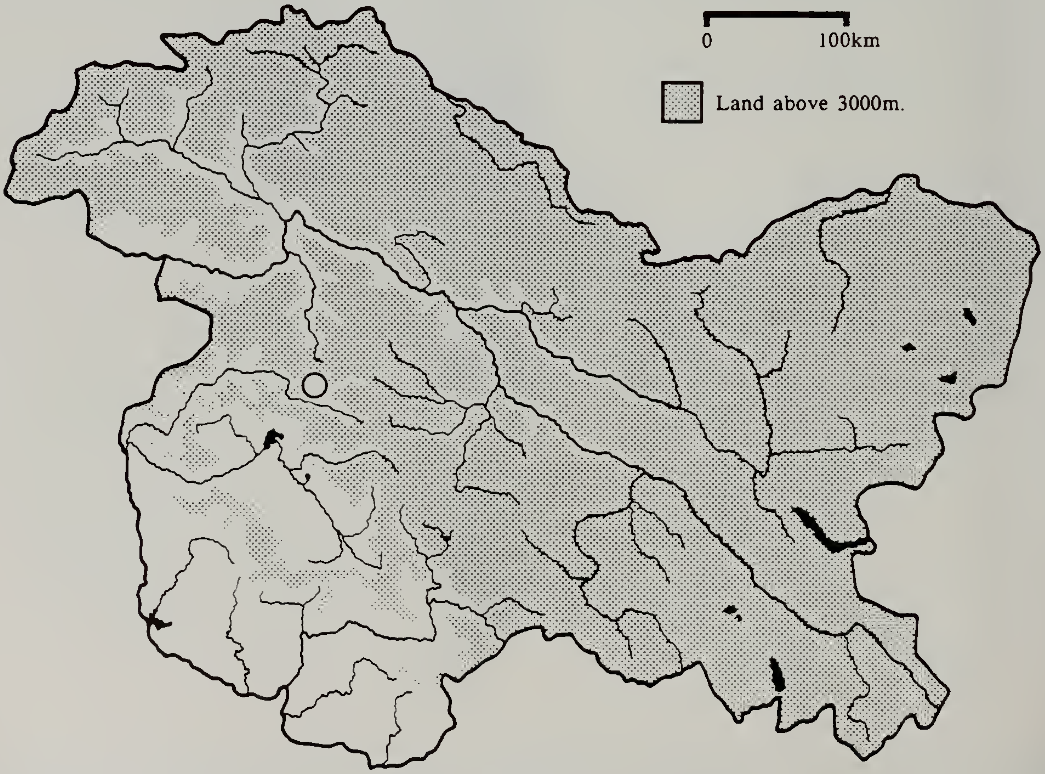
MALE

Figs 254–257 Colour patterns of *B. marussinus* from localities in Kashmir: (254) Chhantir Gah 5–7.viii.1954, (255) Holojut 13–14.viii.1954, (256) Batakush 8.ix.1954, (257) Chhantir Gah 5–7.viii.1954 (for the colour key see Fig. 258).



Map 11 Summary of the world-wide distribution of *B. bohemicus* (for an explanation of the symbols see Map 5).



Map 12 Distribution of *B. bohemicus* in Kashmir (see Map 6).

COLOUR KEY

□ grey-white/cream-white
▢ lemon yellow/golden yellow
▒ light brown
▦ chocolate brown
▥ orange-red
▩ dense mixture of black hairs
■ black

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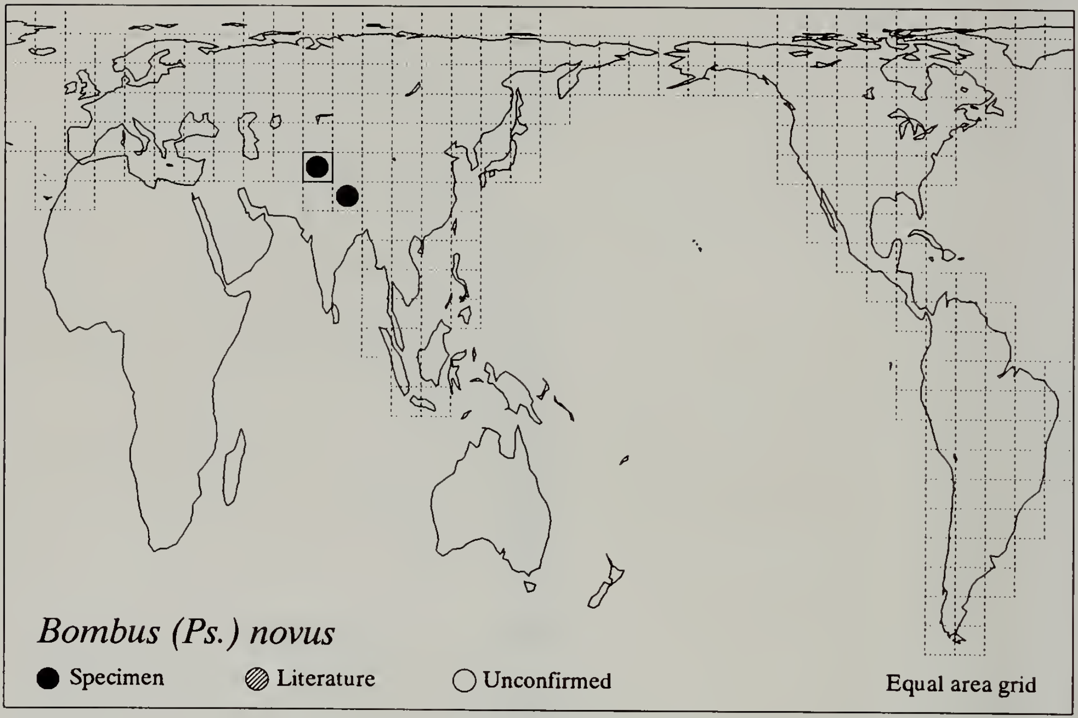
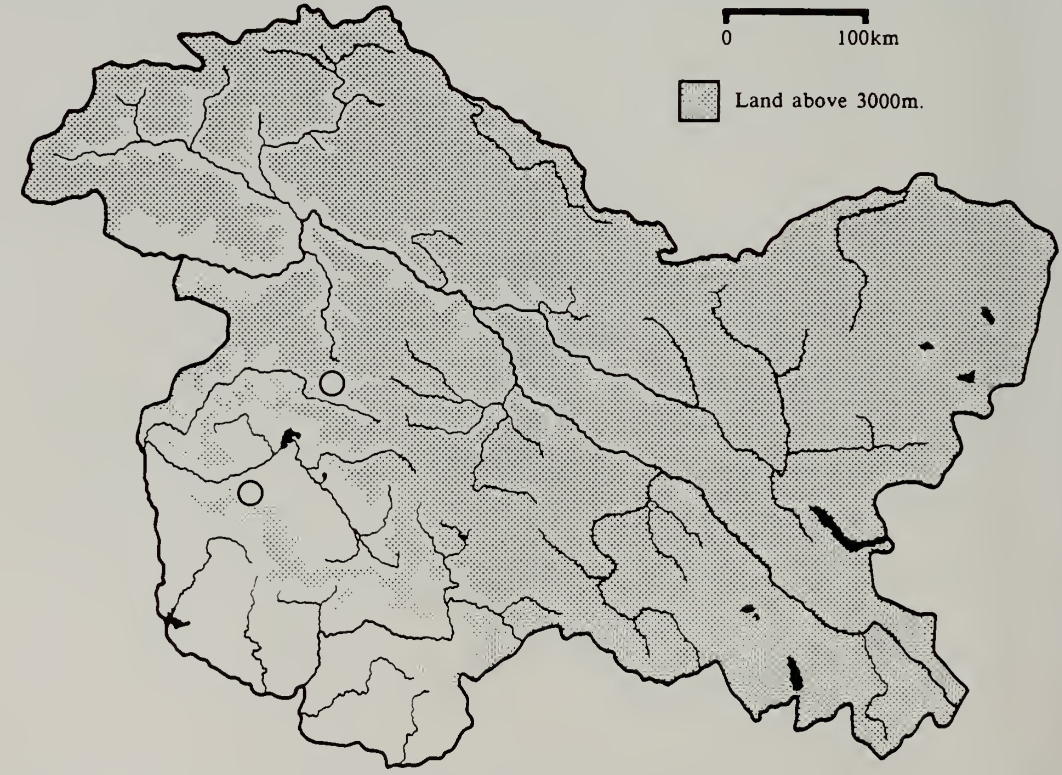
MALE

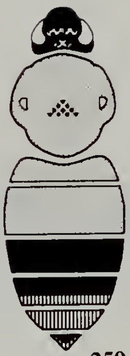
Fig. 258 Colour pattern of *B. bohemicus* from Kashmir: Lal Pani 2–3.ix.1953



Map 13 Summary of the world-wide distribution of *B. novus* (for an explanation of the symbols see Map 5).



Map 14 Distribution of *B. novus* in Kashmir (see Map 6).



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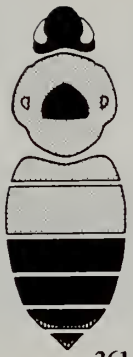

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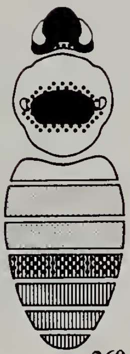
FEMALES



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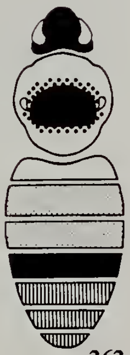
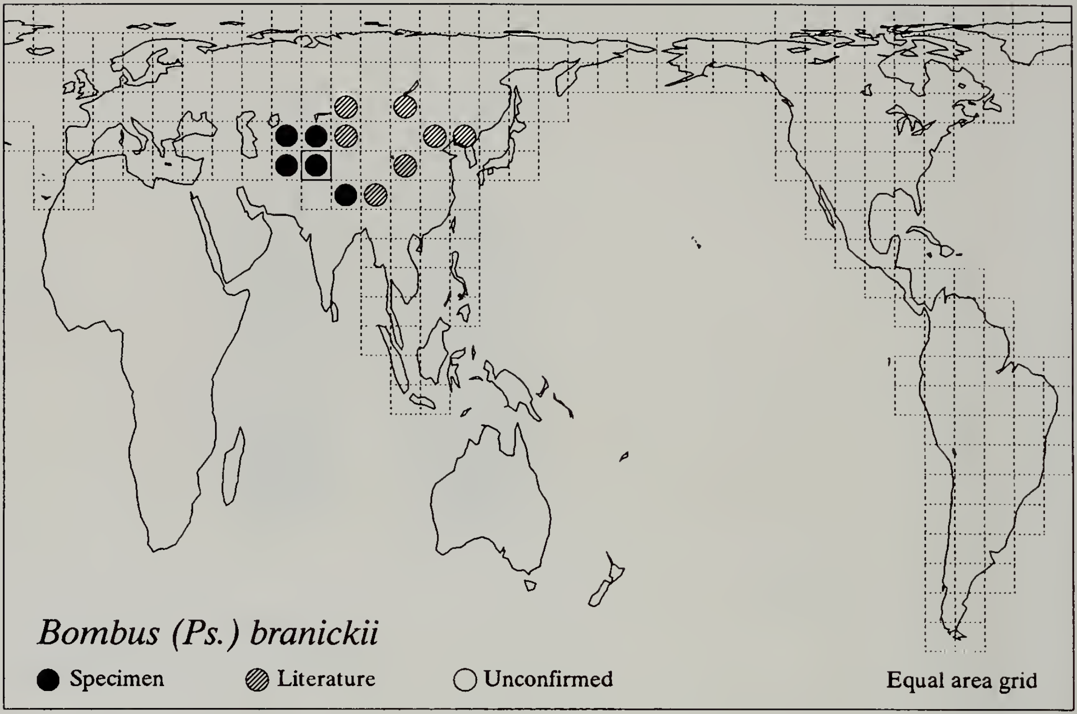


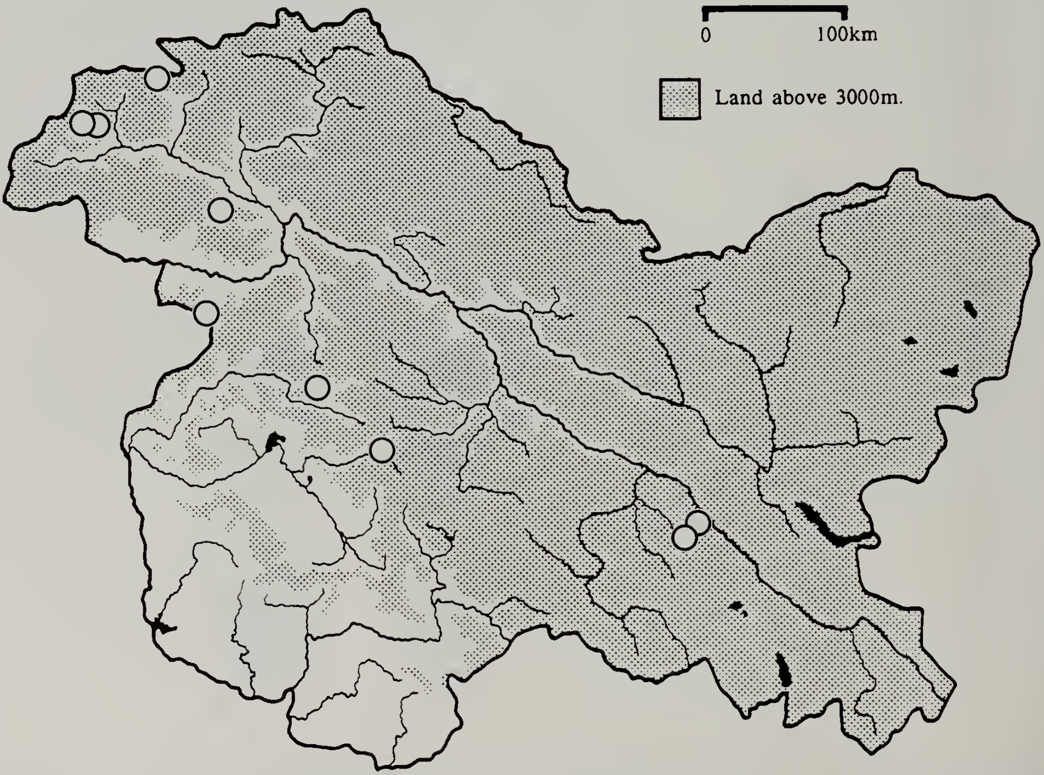
262

MALES

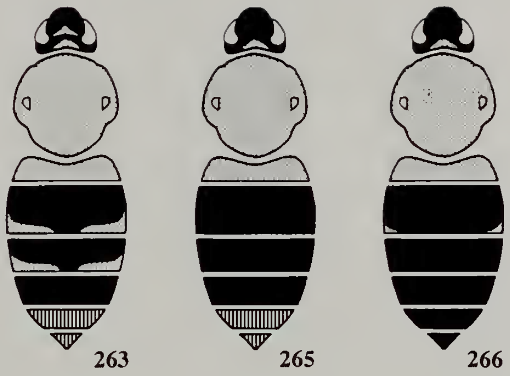
Figs 259–262 Colour patterns of *B. novus* from localities in Kashmir: (259) Apharwat 25.vii.1986, (260) Apharwat 23.viii.1985, (261) Apharwat 25.vii.1986, (262) Apharwat 23.viii.1985 (for the colour key see Fig. 258).



Map 15 Summary of the world-wide distribution of *B. branickii* (for an explanation of the symbols see Map 5).



Map 16 Distribution of *B. branickii* in Kashmir (see Map 6).



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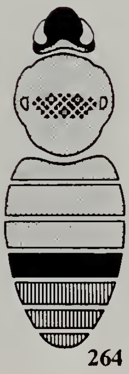
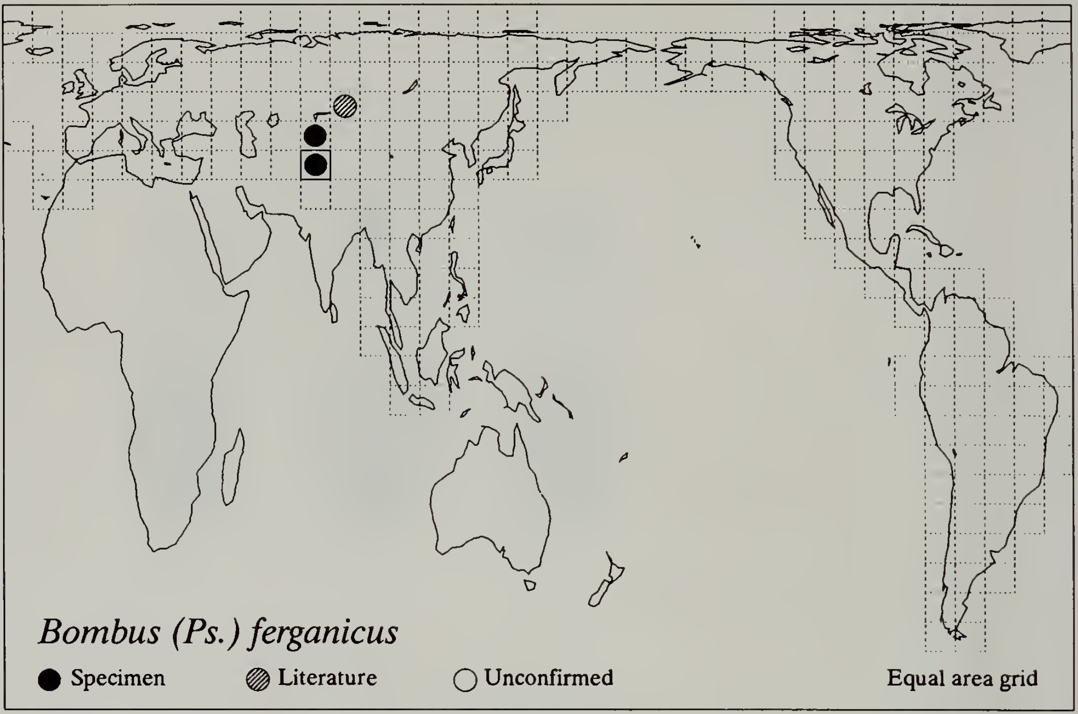
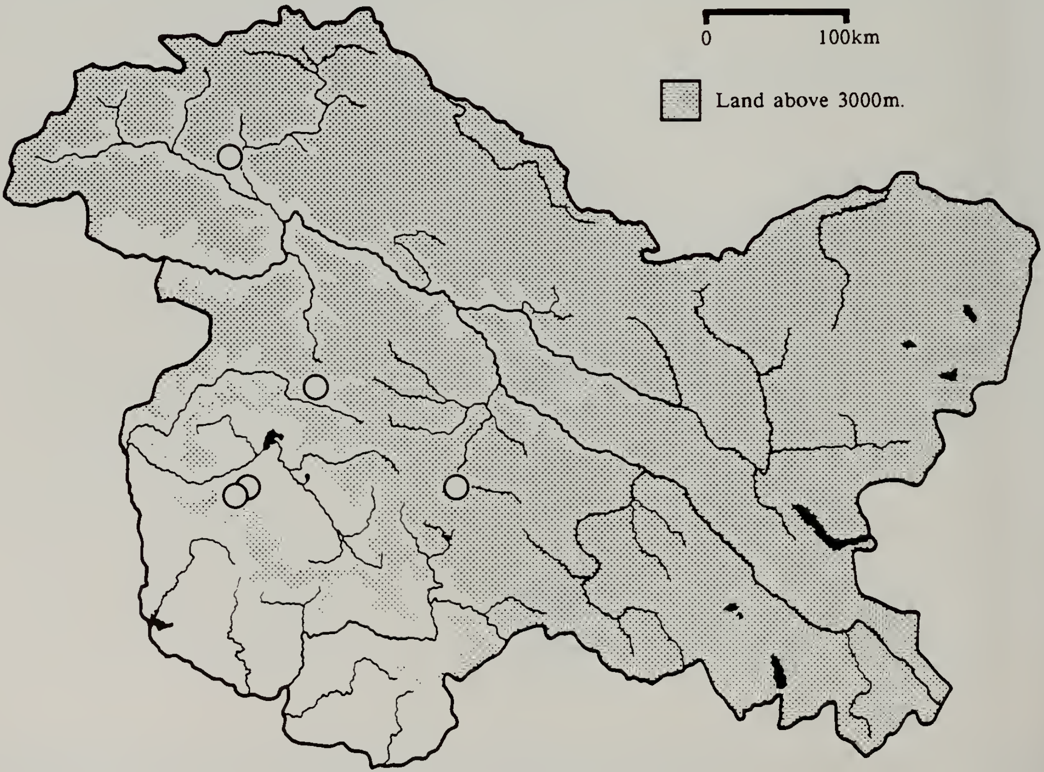


MALE

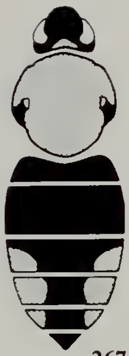
Figs 263–266 Colour patterns of *B. branickii* from localities in Kashmir: (263) Nimaling 19.vii.1980, (264) Chogdo 24.ix.1986, (265) Nimaling 17.vii.1980, (266) Atro Sar 11.viii.1954 (for the colour key see Fig. 258).



Map 17 Summary of the world-wide distribution of *B. ferganicus* (for an explanation of the symbols see Map 5).



Map 18 Distribution of *B. ferganicus* in Kashmir (see Map 6).



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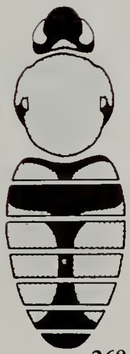

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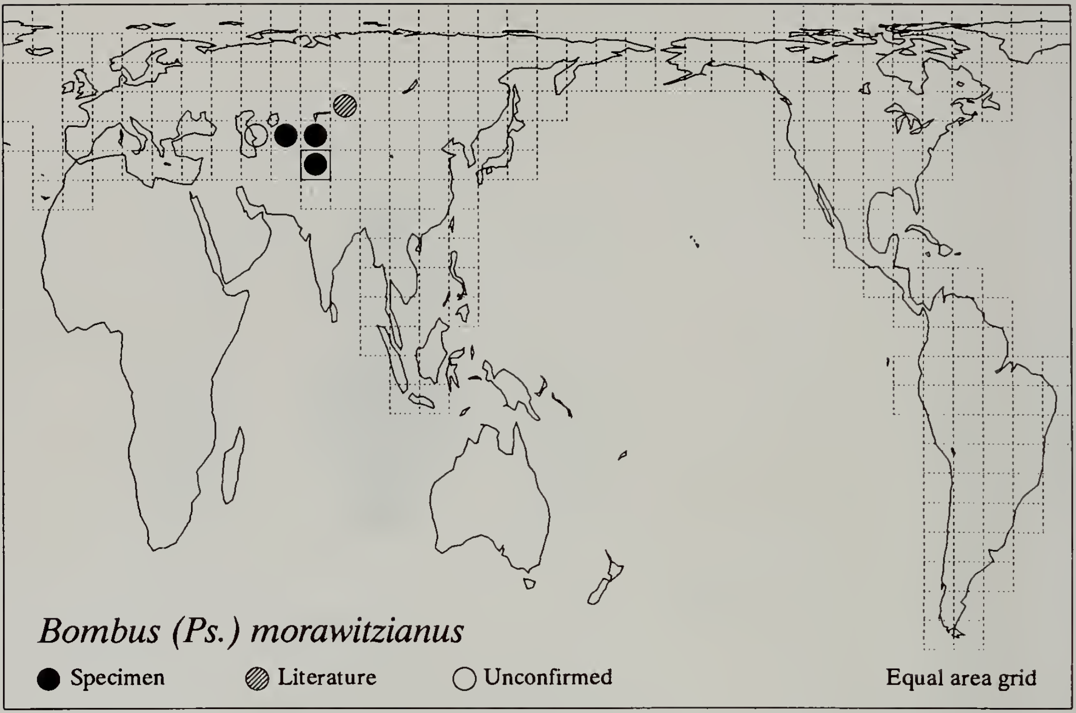
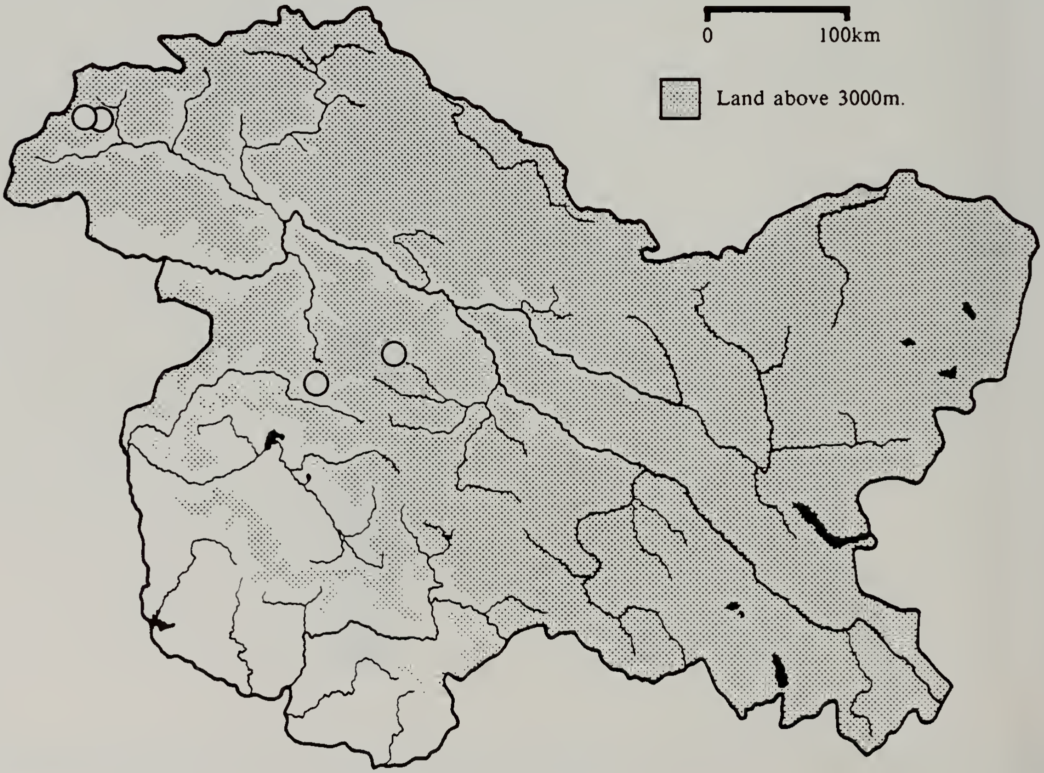
MALE

Figs 267, 268 Colour patterns of *B. ferganicus* from localities in Kashmir: (267) Gulmarg viii.1985, (268) Gulmarg viii.1985 (for the colour key see Fig. 258).



Map 19 Summary of the world-wide distribution of *B. morawitzianus* (for an explanation of the symbols see Map 5).



Map 20 Distribution of *B. morawitzianus* in Kashmir (see Map 6).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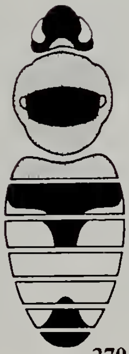
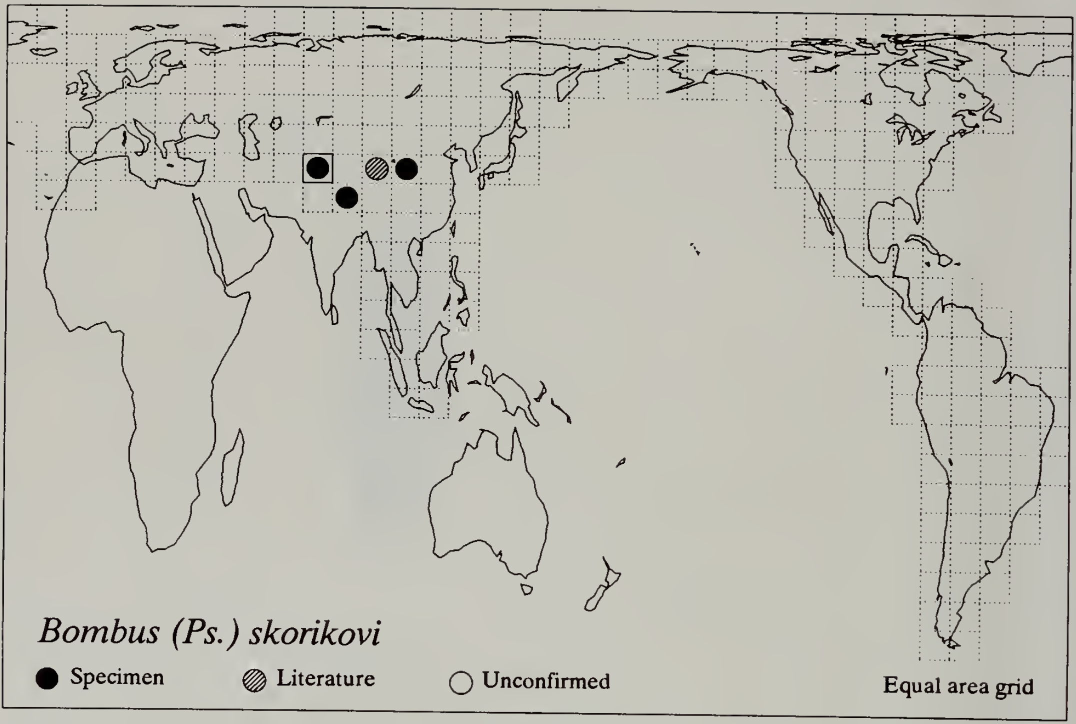
FEMALE

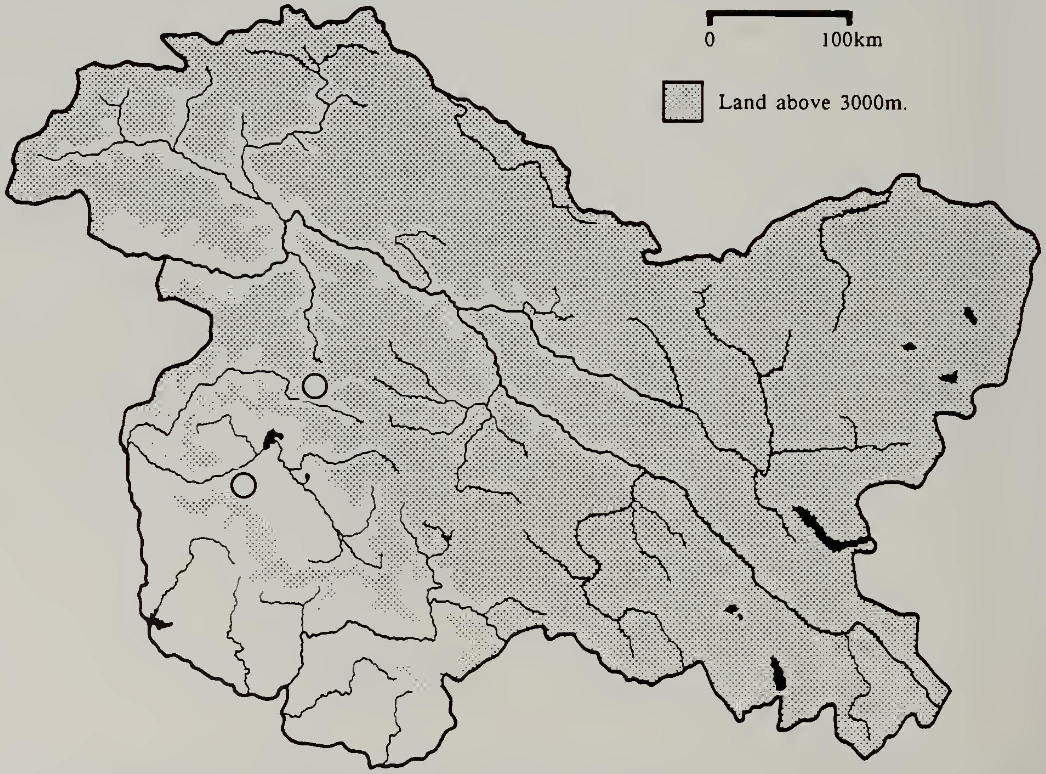

270

MALE

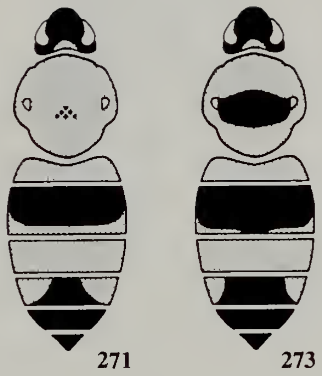
Figs 269, 270 Colour patterns of *B. morawitzianus* from localities in Kashmir: (269) Lal Pani 2–3.ix.1953, (270) Lal Pani 2–3.ix.1953 (for the colour key see Fig. 258).



Map 21 Summary of the world-wide distribution of *B. skorikovi* (for an explanation of the symbols see Map 5).



Map 22 Distribution of *B. skorikovi* in Kashmir (see Map 6).



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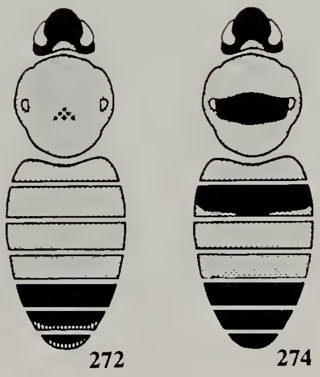
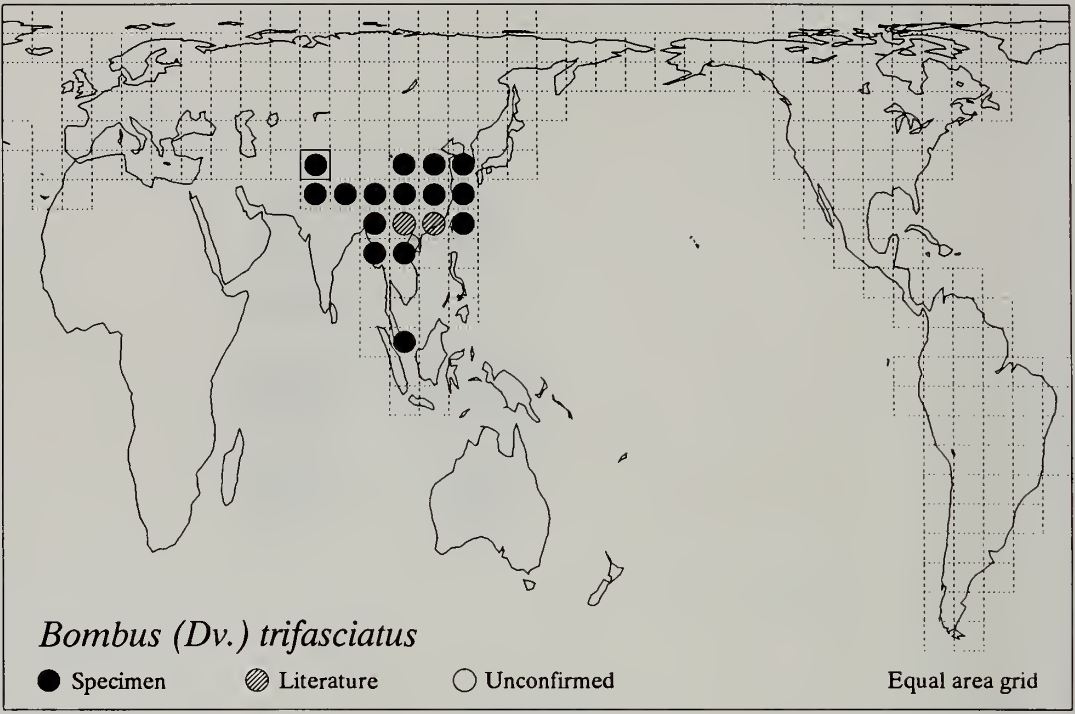
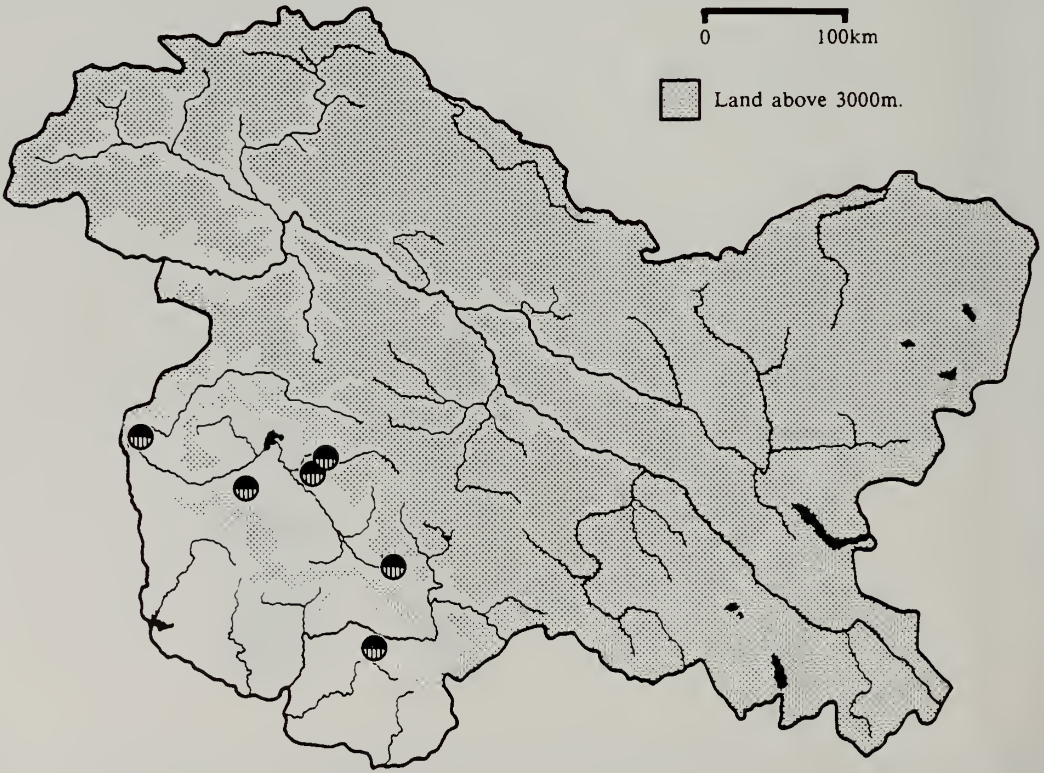


MALES

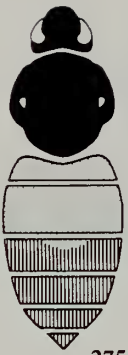
Figs 271–274 Colour patterns of *B. skorikovi* from localities in Kashmir: (271) Lal Pani 2–3.ix.1953, (272) Lal Pani 2–3.ix.1953, (273) Apharwat viii.1985, (274) Lal Pani 2–3.ix.1953 (for the colour key see Fig. 258).



Map 23 Summary of the world-wide distribution of *B. trifasciatus* (for an explanation of the symbols see Map 5).



Map 24 Distribution of *B. trifasciatus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 275–278).



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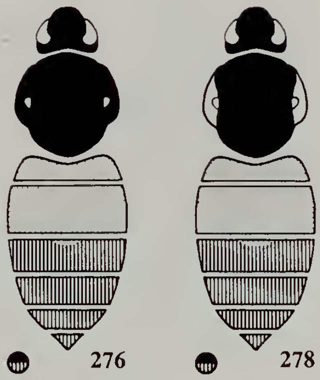

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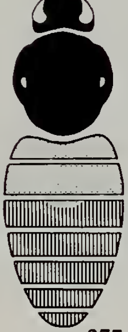

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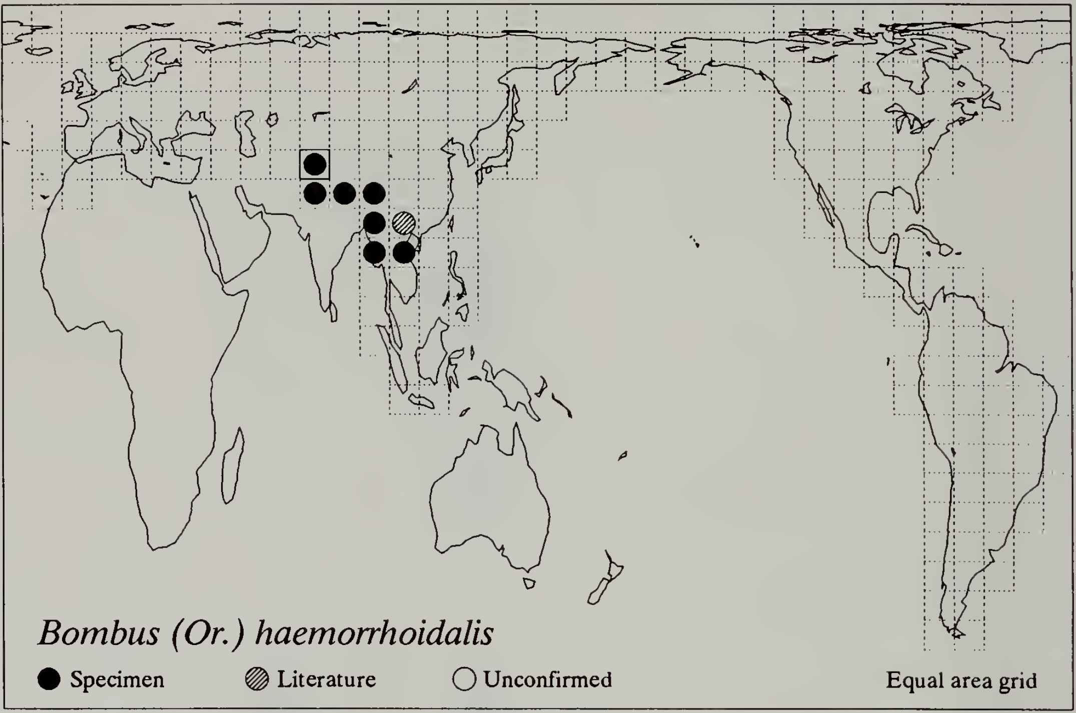
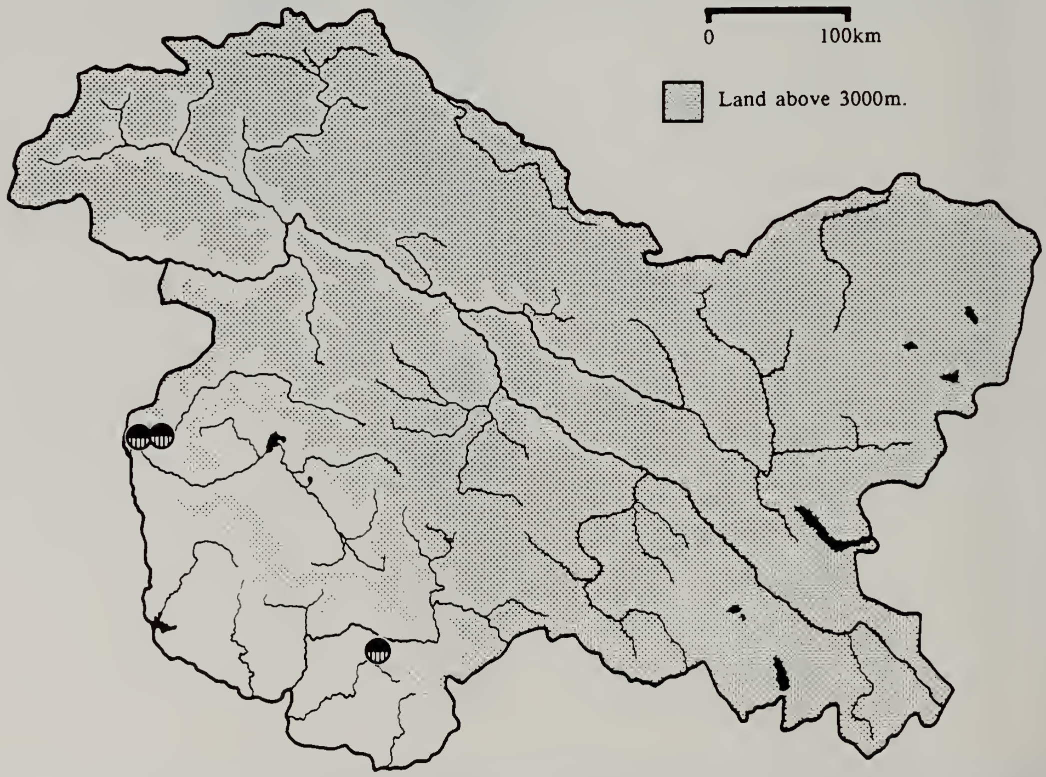
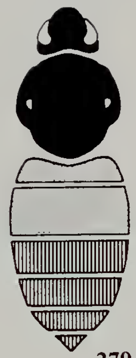
Figs 275–278 Colour patterns of *B. trifasciatus* from localities in Kashmir: (275) Gulmarg 28.vii.1985, (276) Patnitop 6.ix.1986, (277) Harwan 24.viii.1980, (278) Gulmarg 1913 (for the colour key see Fig. 258).



Map 25 Summary of the world-wide distribution of *B. haemorrhoidalis* (for an explanation of the symbols see Map 5).



Map 26 Distribution of *B. haemorrhoidalis* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 279–281).



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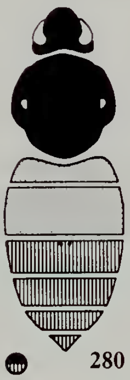

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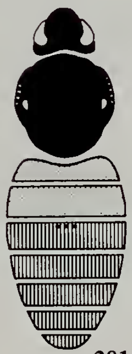

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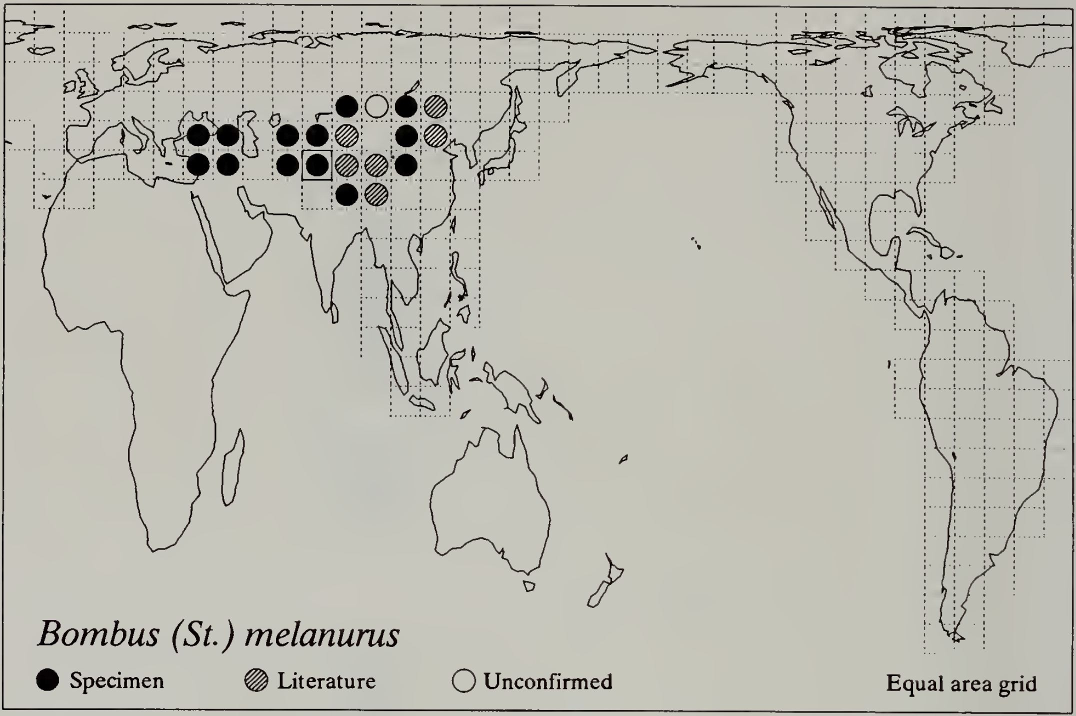
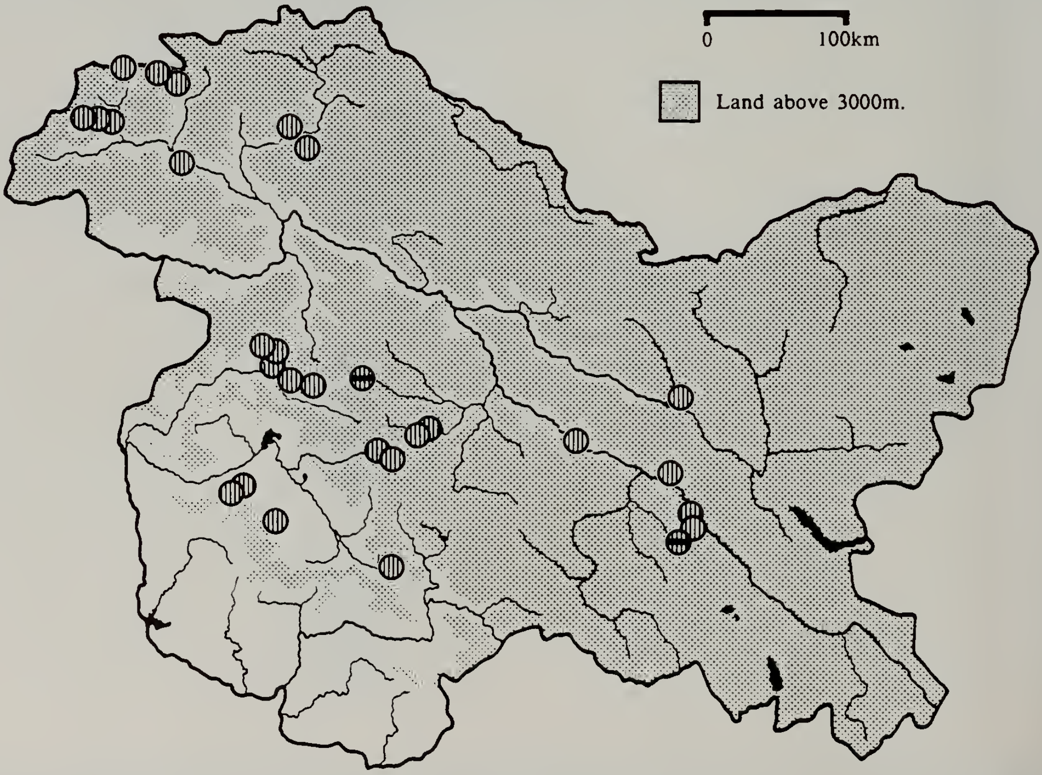
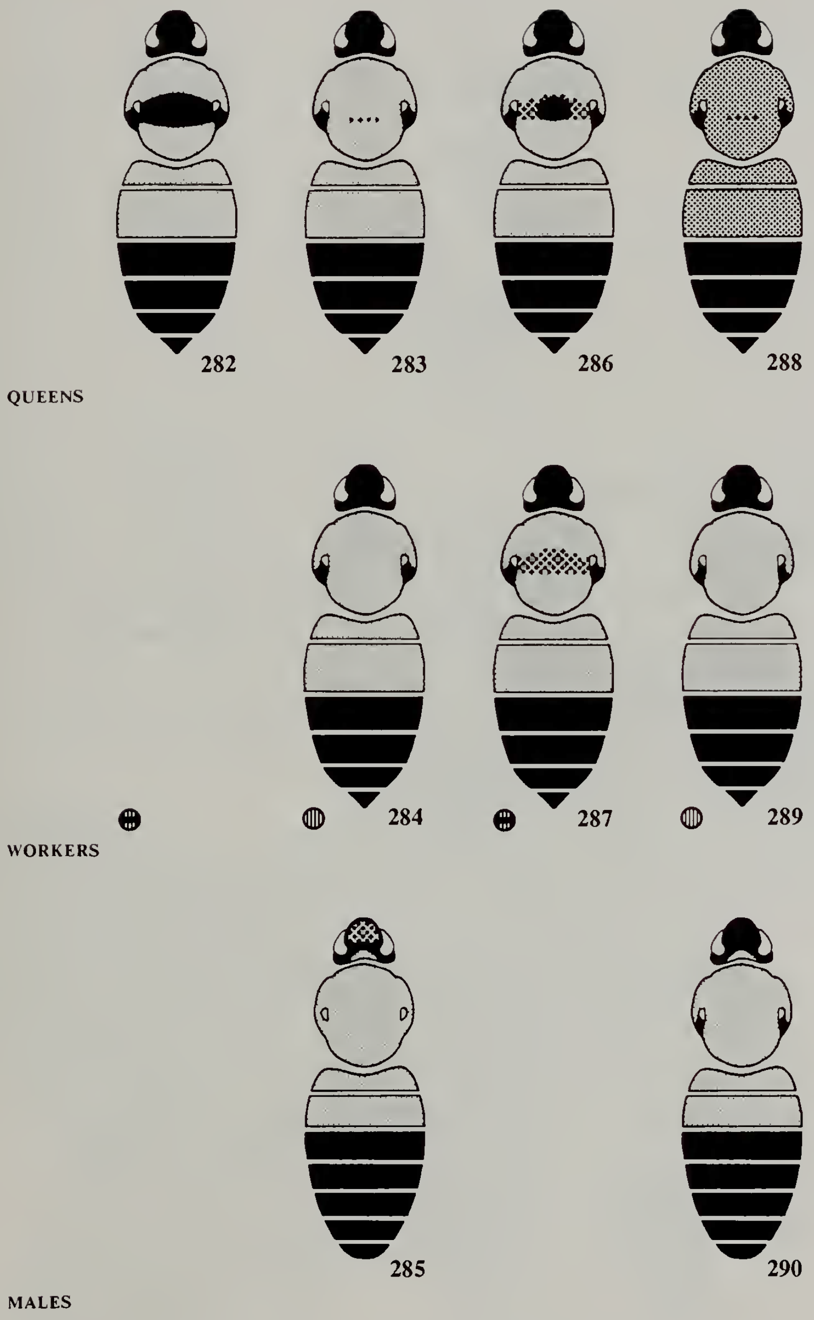
Figs 279–281 Colour patterns of *B. haemorrhoidalis* from localities in Kashmir: (279) Muzaffarabad 10–12.v.1954, (280) Patnitop 6–8.ix.1986, (281) Muzaffarabad 15.x.1953 (for the colour key see Fig. 258).



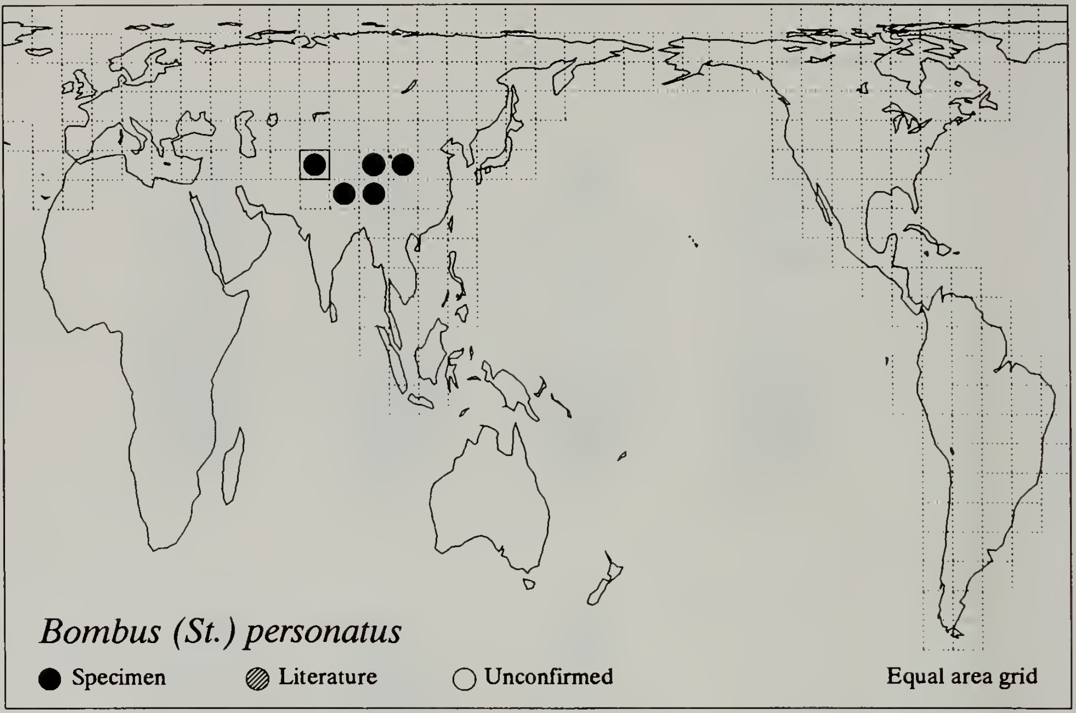
Map 27 Summary of the world-wide distribution of *B. melanurus* (for an explanation of the symbols see Map 5).



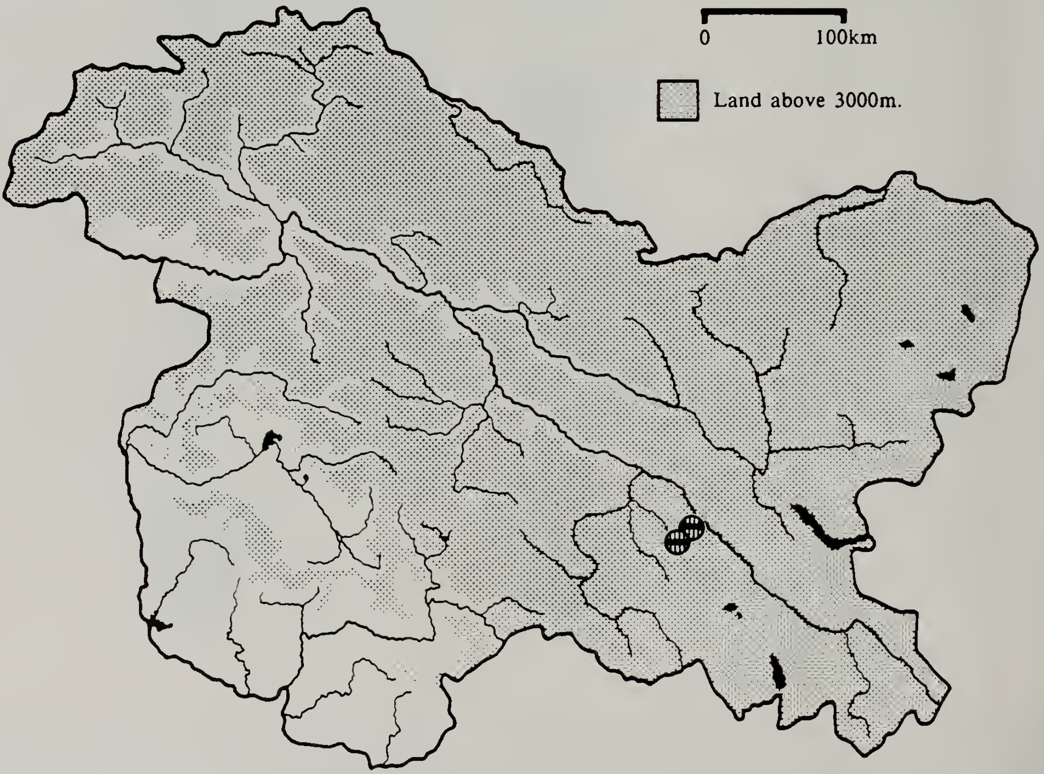
Map 28 Distribution of *B. melanurus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 282–290).



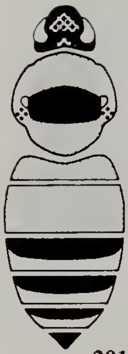
Figs 282–290 Colour patterns of *B. melanurus* from localities in Kashmir: (282) Nimaling 18.vii.1980, (283) Leh 9.vii.1980, (284) Leh 3.vii.1980, (285) Chogdo 24.ix.1986, (286) Chittakatha Sar 19–24.viii.1953, (287) Gulmarg viii.1986, (288) Gulmarg 13.viii.1980, (289) Gulmarg 16.viii.1980, (290) Gulmarg viii.1985 (for the colour key see Fig. 258).



Map 29 Summary of the world-wide distribution of *B. personatus* (for an explanation of the symbols see Map 5).



Map 30 Distribution of *B. personatus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 291–294).



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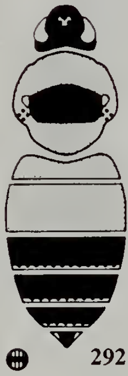

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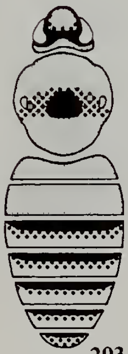
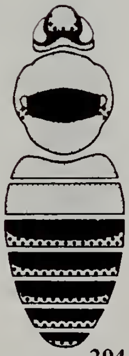


293



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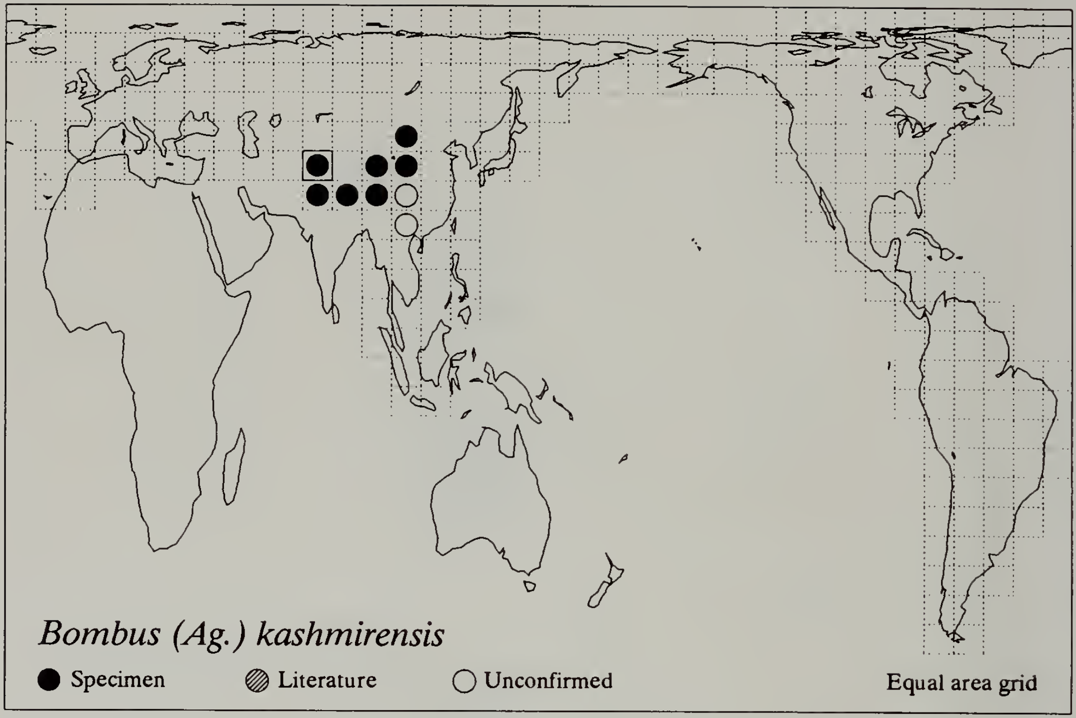
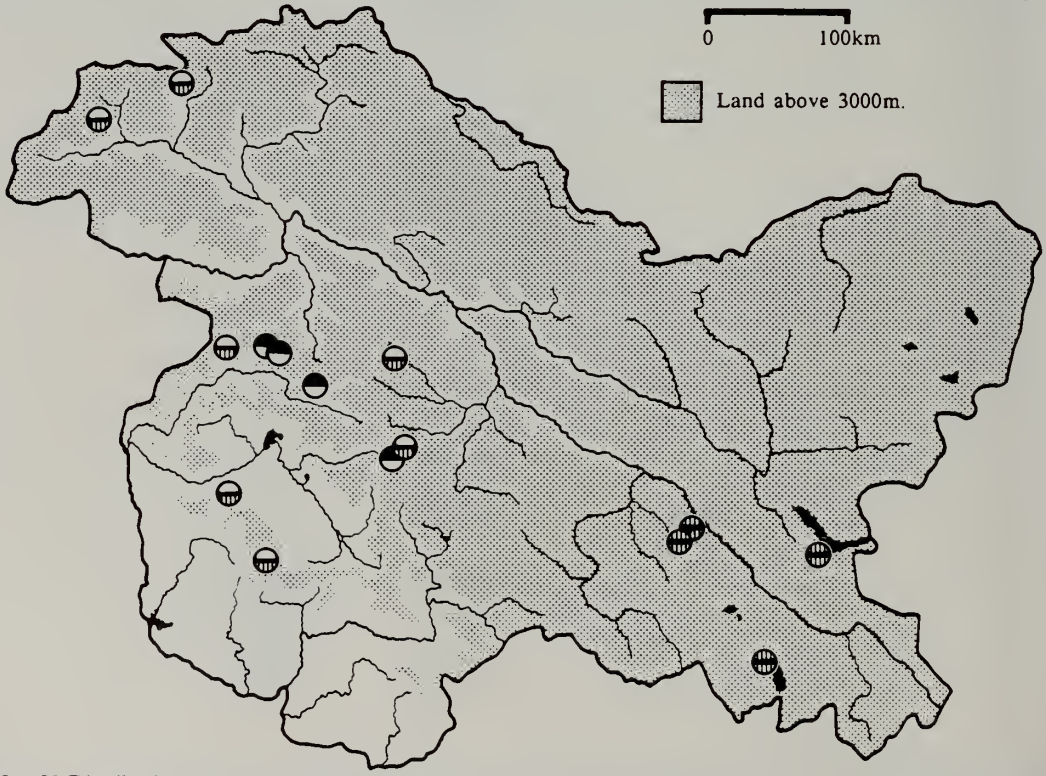
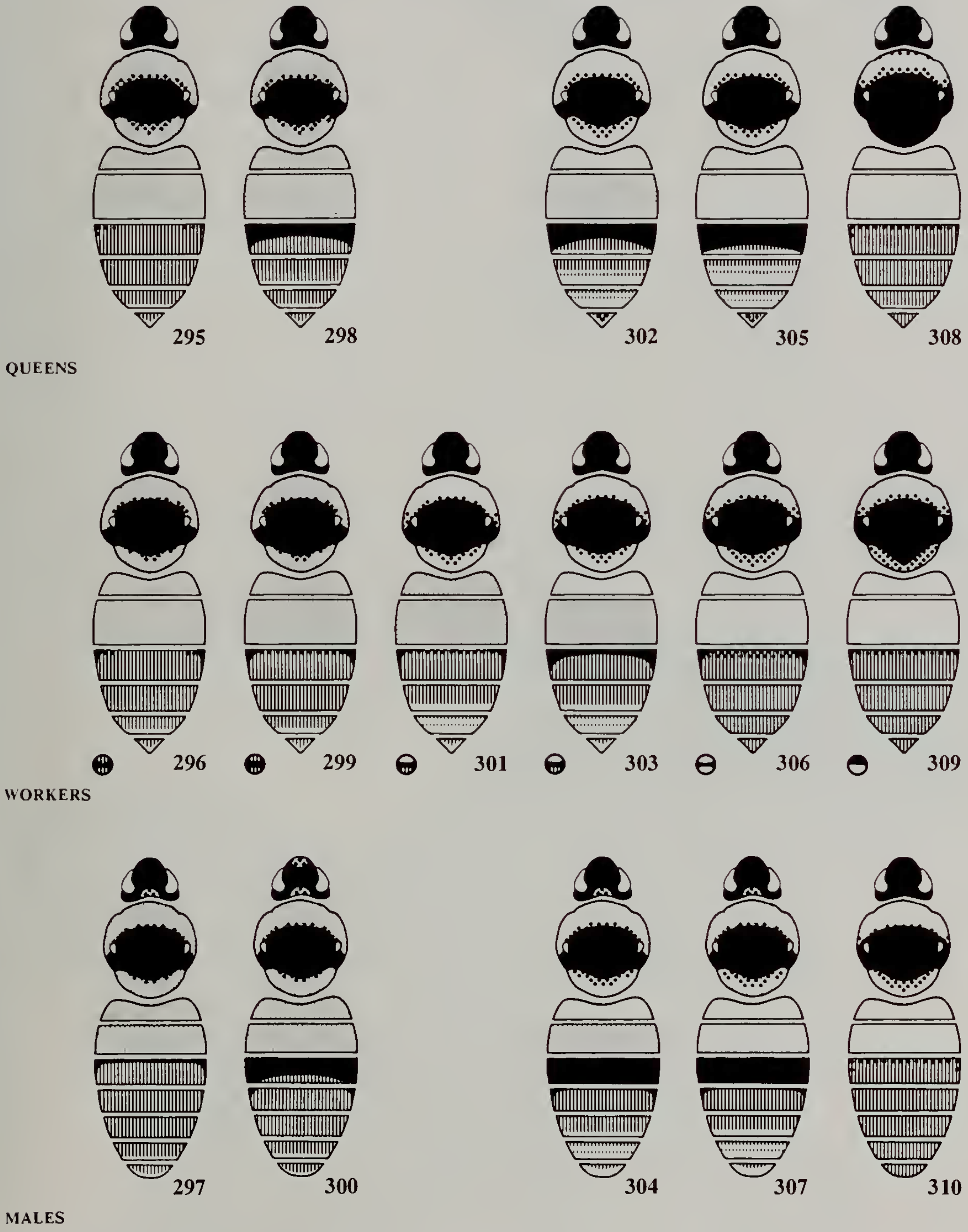
Figs 291–294 Colour patterns of *B. personatus* from localities in Kashmir: (291) Nimaling 16.vii.1980, (292) Nimaling 21.vii.1980, (293) Chogdo 24.ix.1986, (294) Chogdo 24.ix.1986 (for the colour key see Fig. 258).



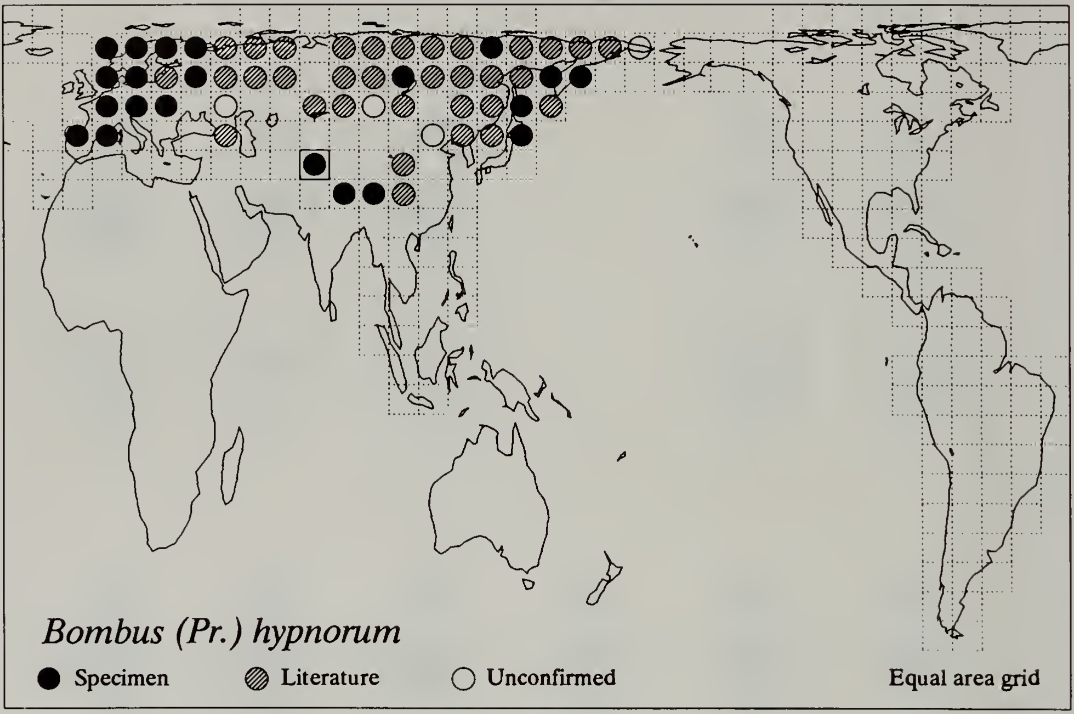
Map 31 Summary of the world-wide distribution of *B. kashmirensis* (for an explanation of the symbols see Map 5).



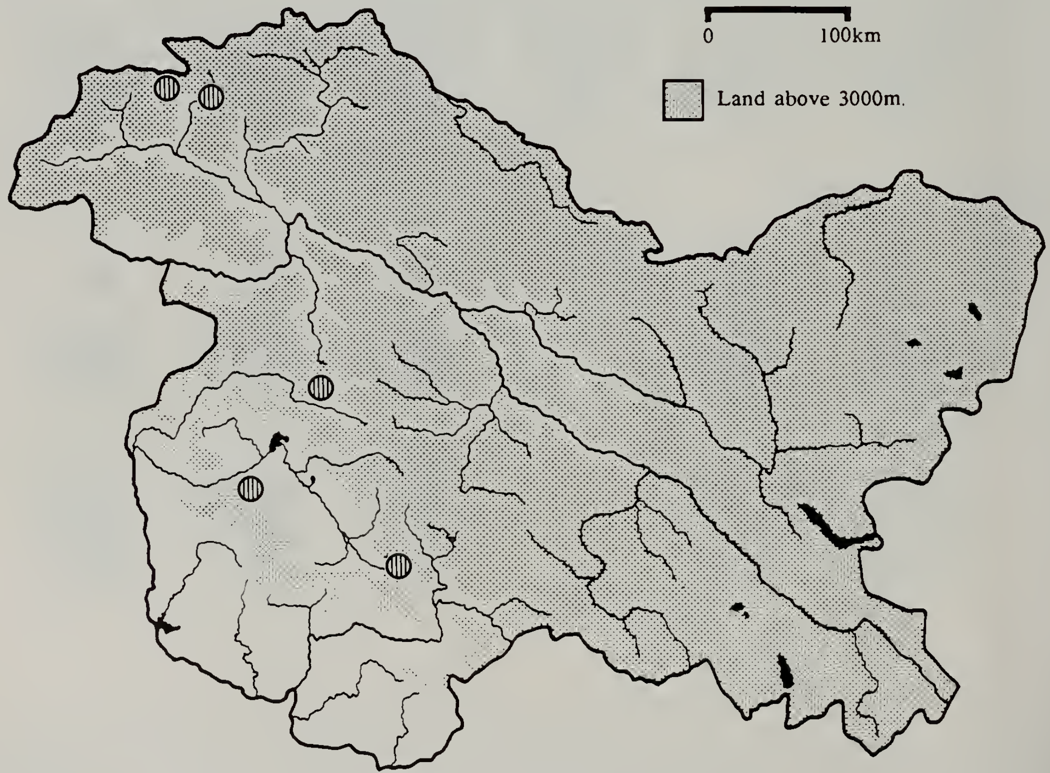
Map 32 Distribution of *B. kashmirensis* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 295–310).



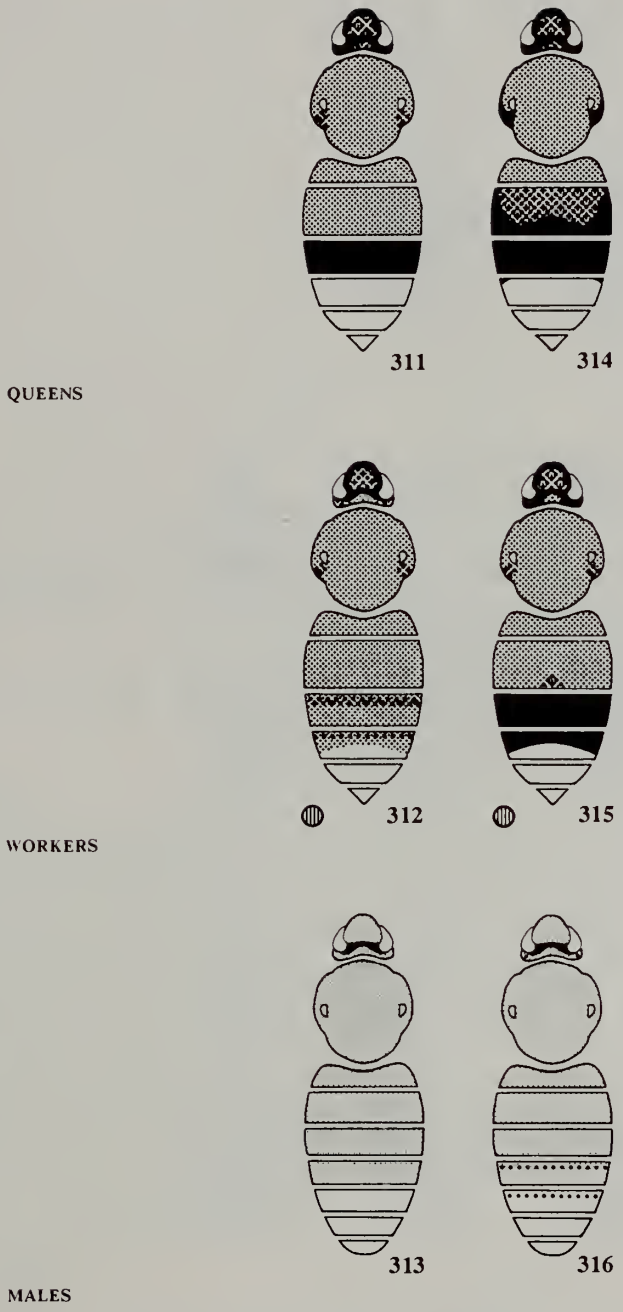
Figs 295–310 Colour patterns of *B. kashmirensis* from localities in Kashmir: (295) Nimaling 20.vii.1980, (296) Nimaling 15.vii.1980, (297) Chogdo 24.ix.1986, (298) Nimaling 20.vii.1980, (299) Nimaling 19.vii.1980, (300) Chogdo 24.ix.1986, (301) Gumri 10–11.viii.1986, (302) Apharwat 24.vii.1986, (303) Apharwat viii.1985, (304) Apharwat 30.viii.1986, (305) Apharwat 24.viii.1986, (306) Apharwat viii.1986, (307) Apharwat 23.viii.1985, (308) Nigagar 17.ix.1986, (309) Nigagar 17.ix.1986, (310) Lal Pani 2–3.ix.1953 (for the colour key see Fig. 258).



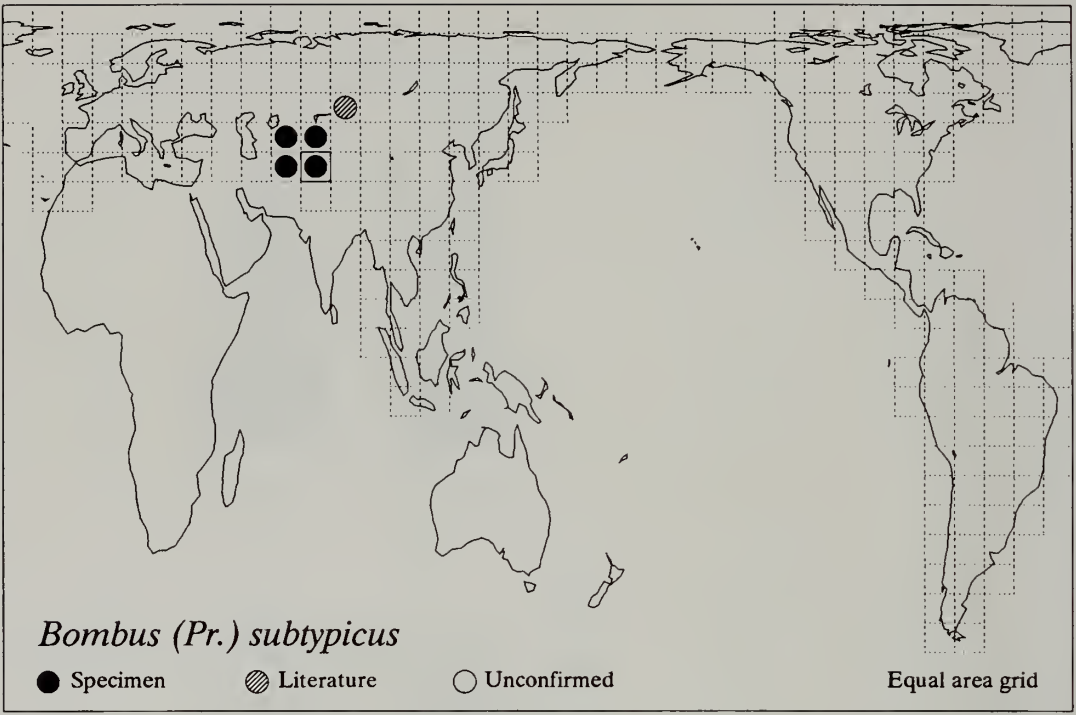
Map 33 Summary of the world-wide distribution of *B. hypnorum* (for an explanation of the symbols see Map 5).



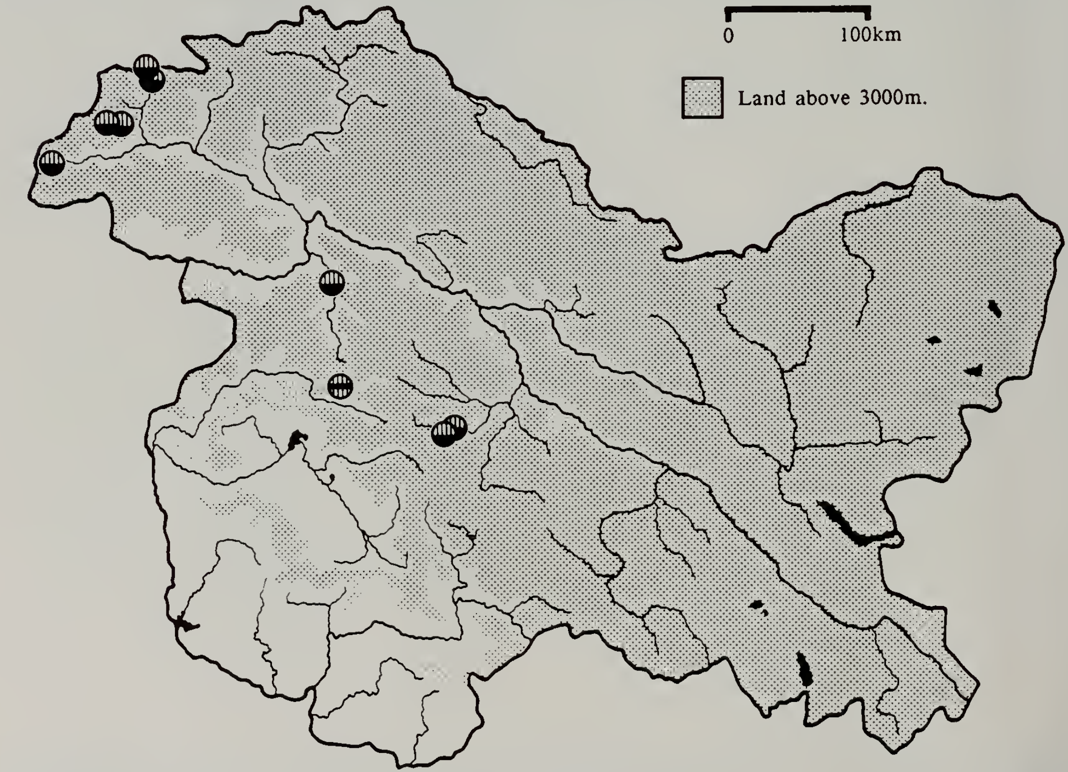
Map 34 Distribution of *B. hypnorum* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 311–316).



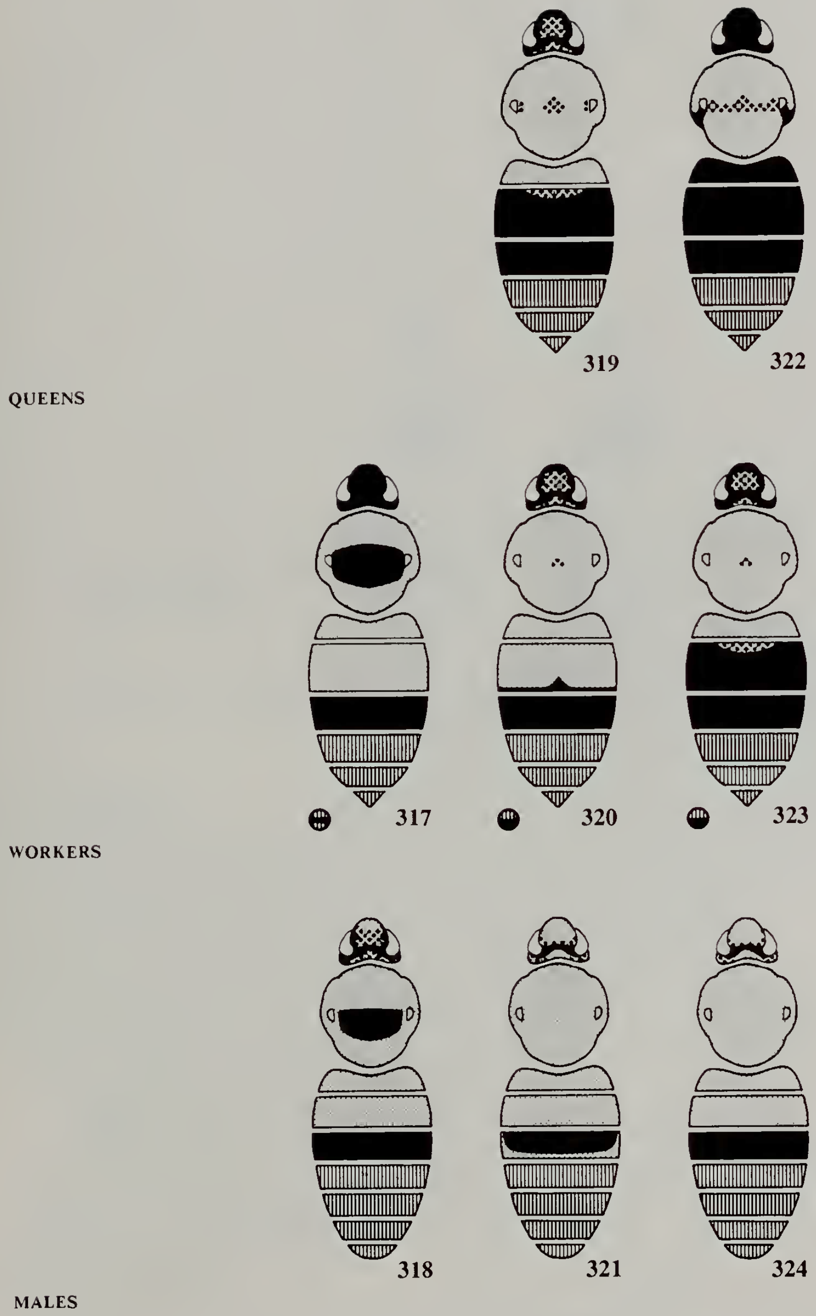
Figs 311–316 Colour patterns of *B. hypnorum* from localities in Kashmir: (311) Apharwat 25.vii.1986, (312) Apharwat viii.1986, (313) Apharwat 16.viii.1980, (314) Apharwat 25.vii.1986, (315) Apharwat viii.1985, (316) Apharwat viii.1985 (for the colour key see Fig. 258).



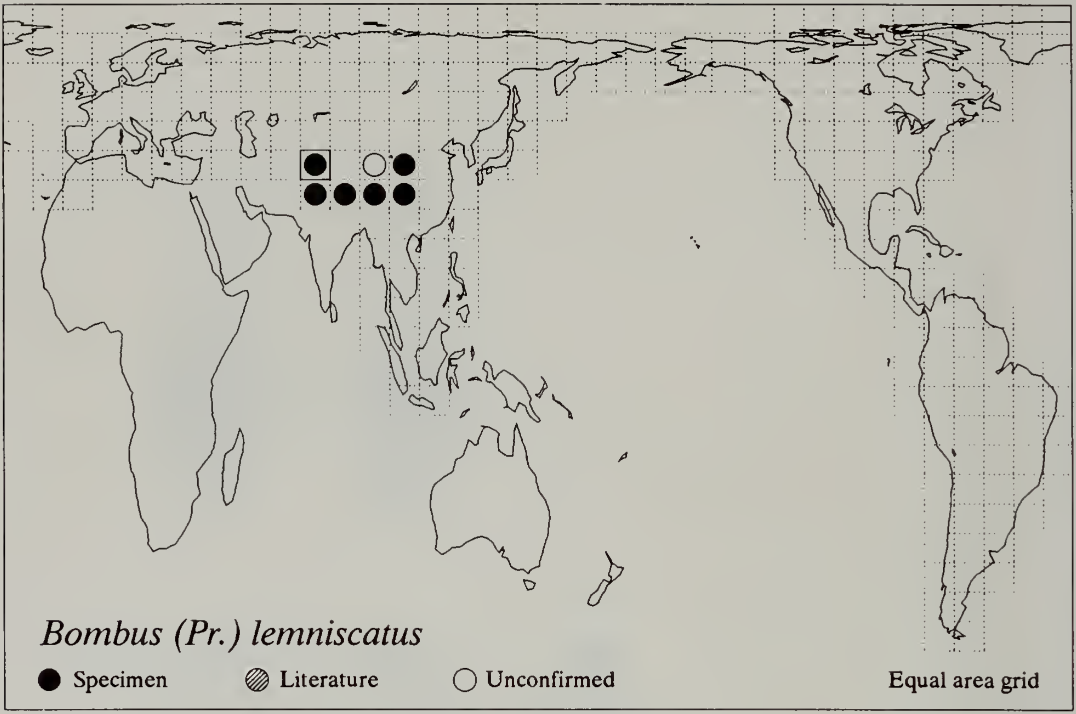
Map 35 Summary of the world-wide distribution of *B. subtypicus* (for an explanation of the symbols see Map 5).



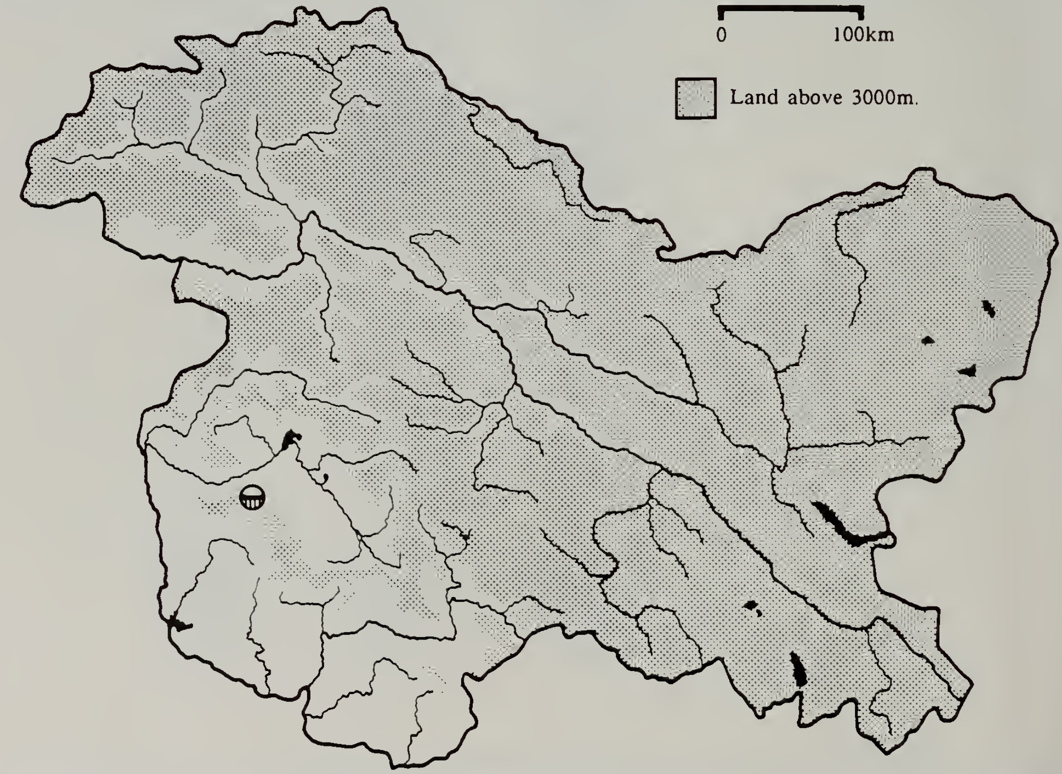
Map 36 Distribution of *B. subtypicus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 317–324).



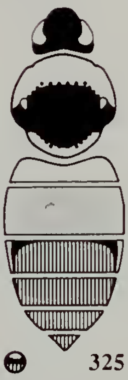
Figs 317–324 Colour patterns of *B. subtypicus* from localities in Kashmir: (317) Lal Pani 2–3.ix.1953, (318) Lal Pani 2–3.ix.1953, (319) Dras 10–11.viii.1986, (320) Dras 10–11.viii.1986, (321) Lal Pani 2–3.ix.1953, (322) Astor 29.v.1954, (323) Dras 10–11.viii.1986, (324) Rawat 20–21.viii.1954 (for the colour key see Fig. 258).



Map 37 Summary of the world-wide distribution of *B. lemniscatus* (for an explanation of the symbols see Map 5).



Map 38 Distribution of *B. lemniscatus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 325 & 326).



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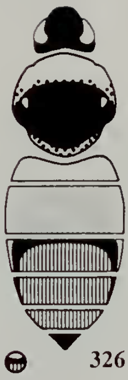

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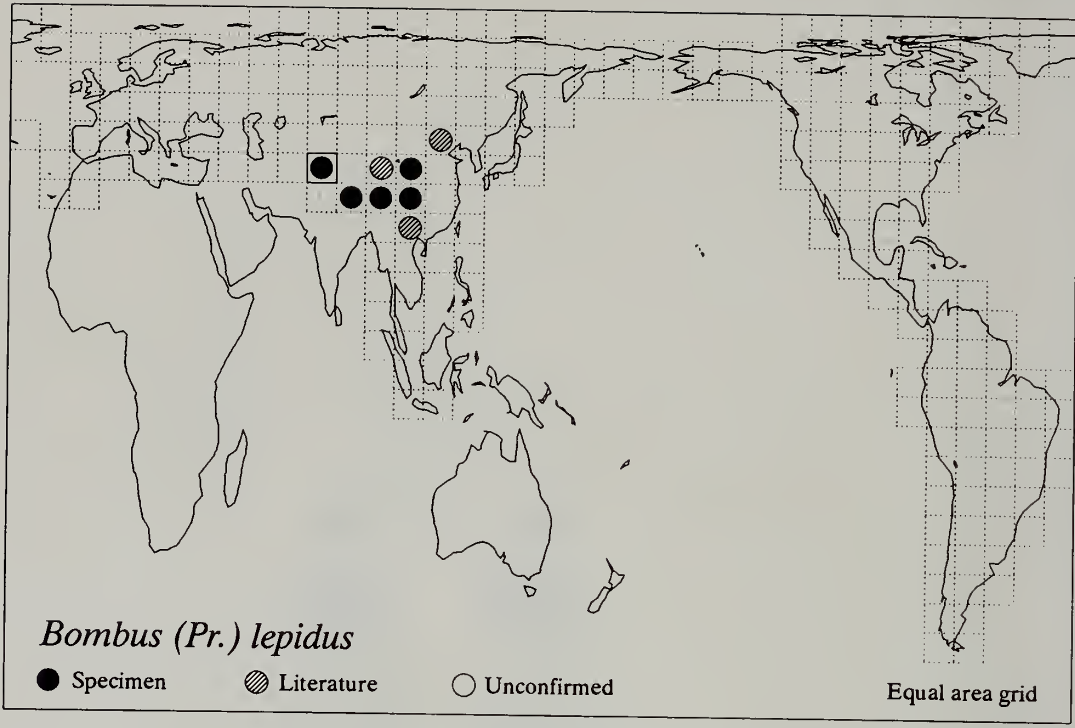
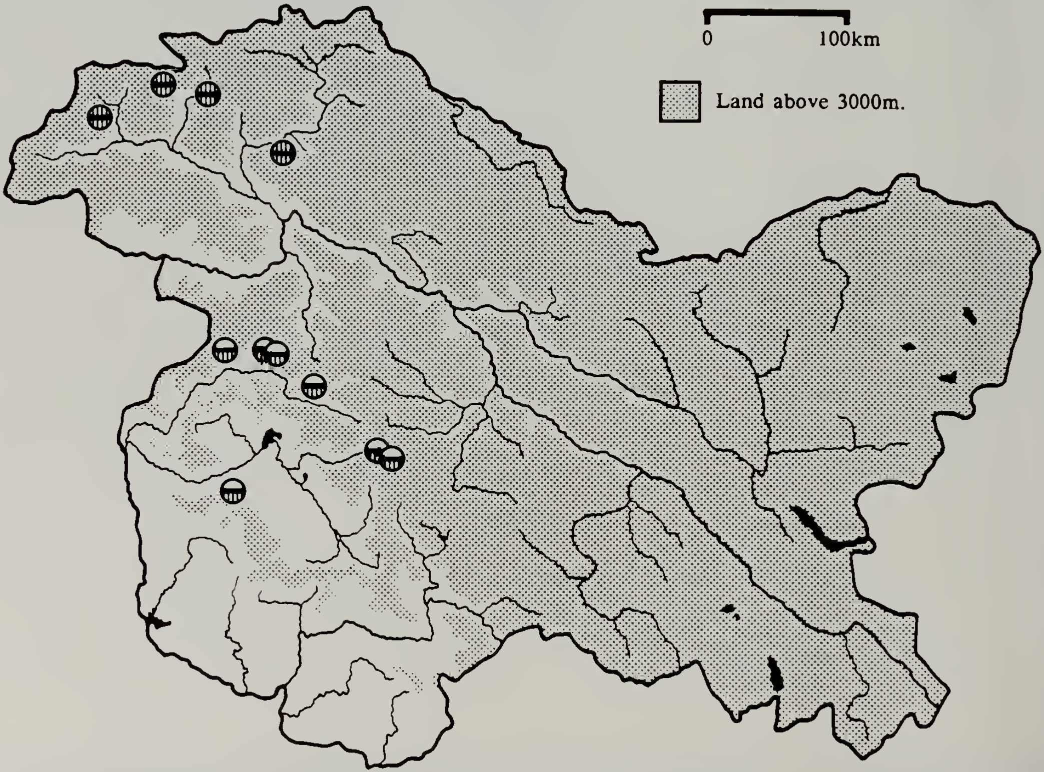
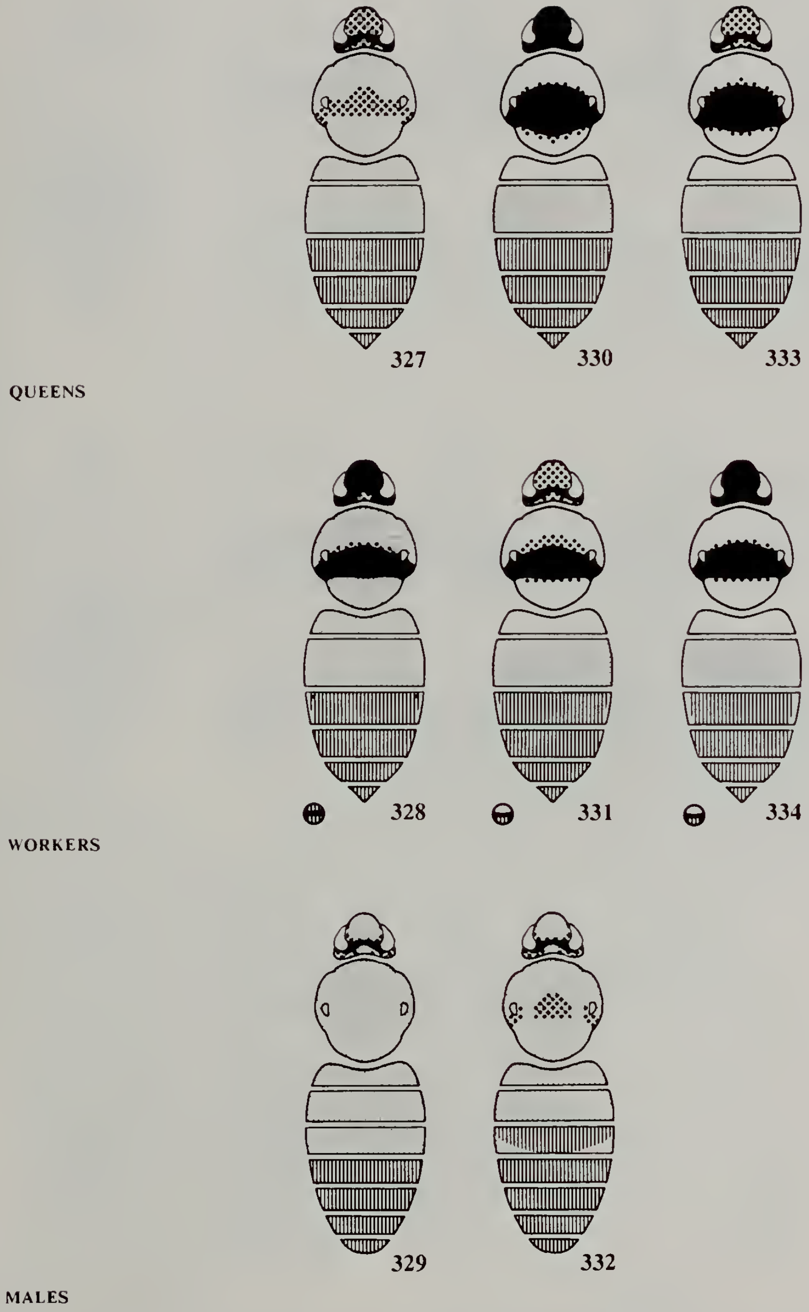
Figs 325, 326 Colour patterns of *B. lemniscatus* from Kashmir: (325) Apharwat viii–ix.1986, (326) Apharwat viii–ix.1986 (for the colour key see Fig. 258).



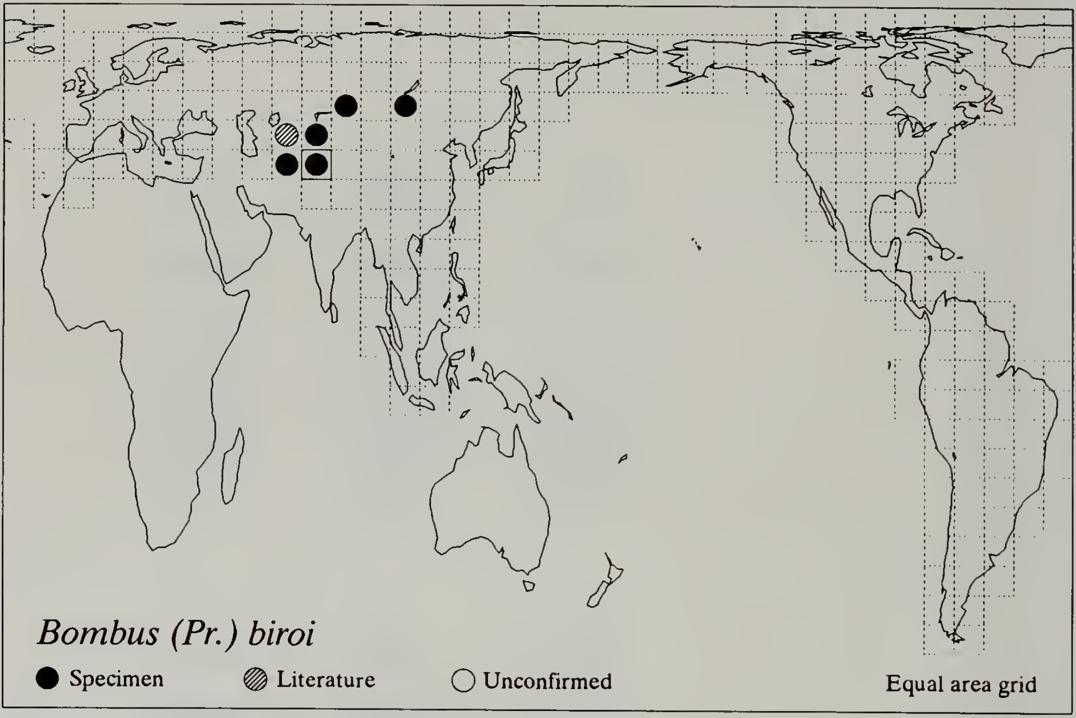
Map 39 Summary of the world-wide distribution of *B. lepidus* (for an explanation of the symbols see Map 5).



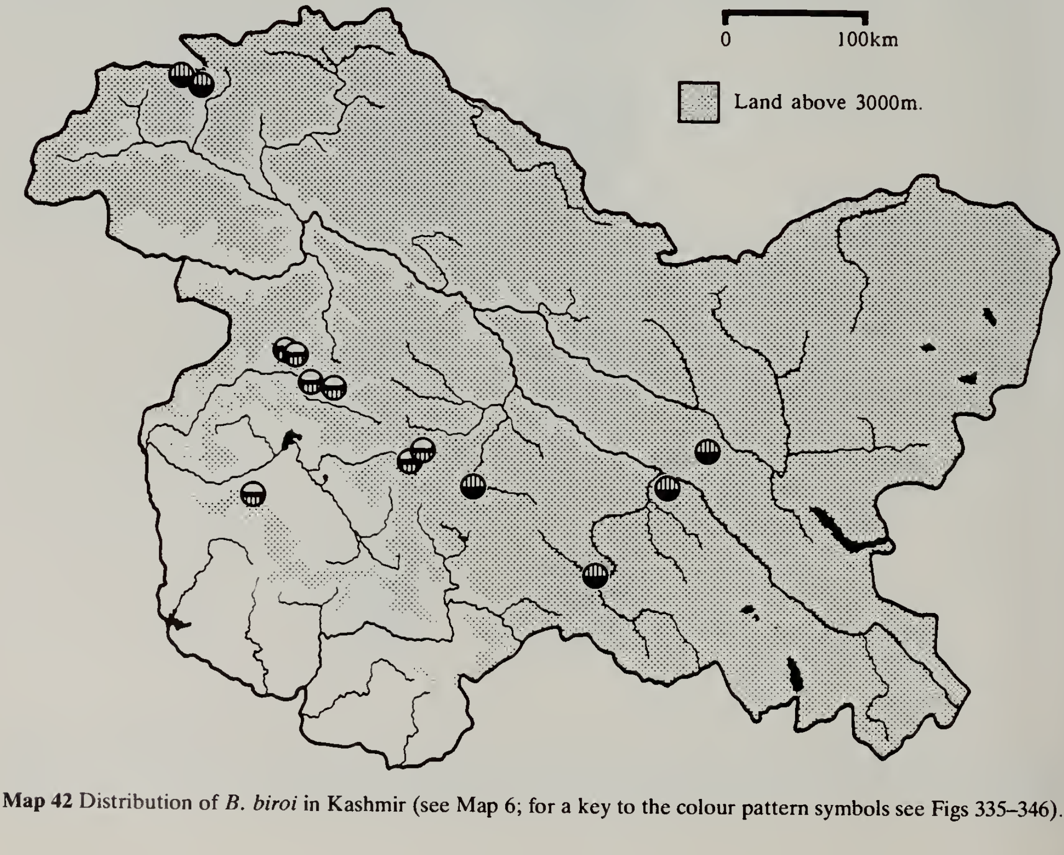
Map 40 Distribution of *B. lepidus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 327–334).



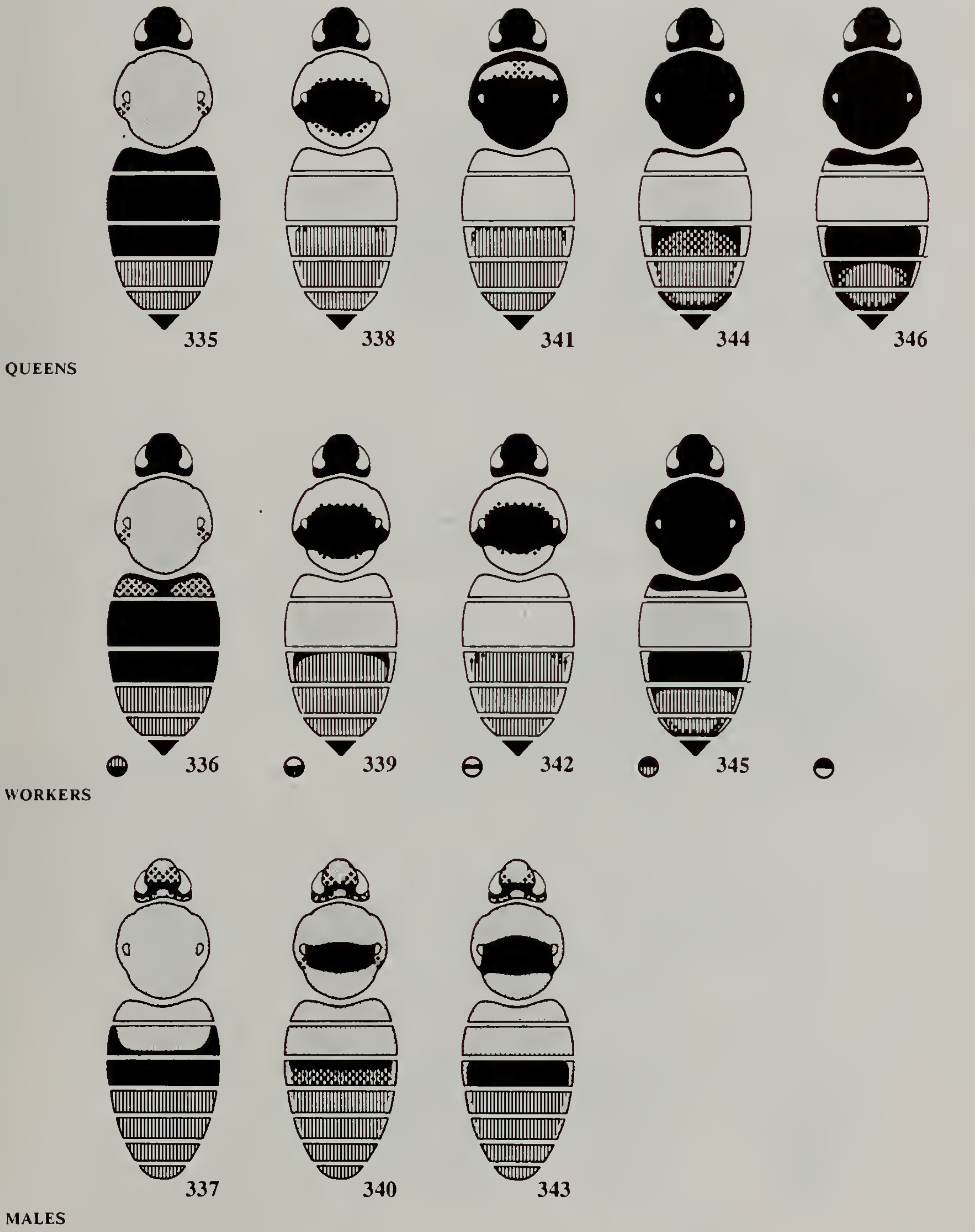
Figs 327–334 Colour patterns of *B. lepidus* from localities in Kashmir: (327) Banidas 30.vi–2.vii.1959, (328) Bulandtar 3.viii.1954, (329) Dalti 7.ix.1954, (330) Lilam 17.viii.1953, (331) Surgun 29–30.vii.1953, (332) Nigagar 17.ix.1986, (333) Apharwat 25.vii.1986, (334) Apharwat viii.1986 (for the colour key see Fig. 258).



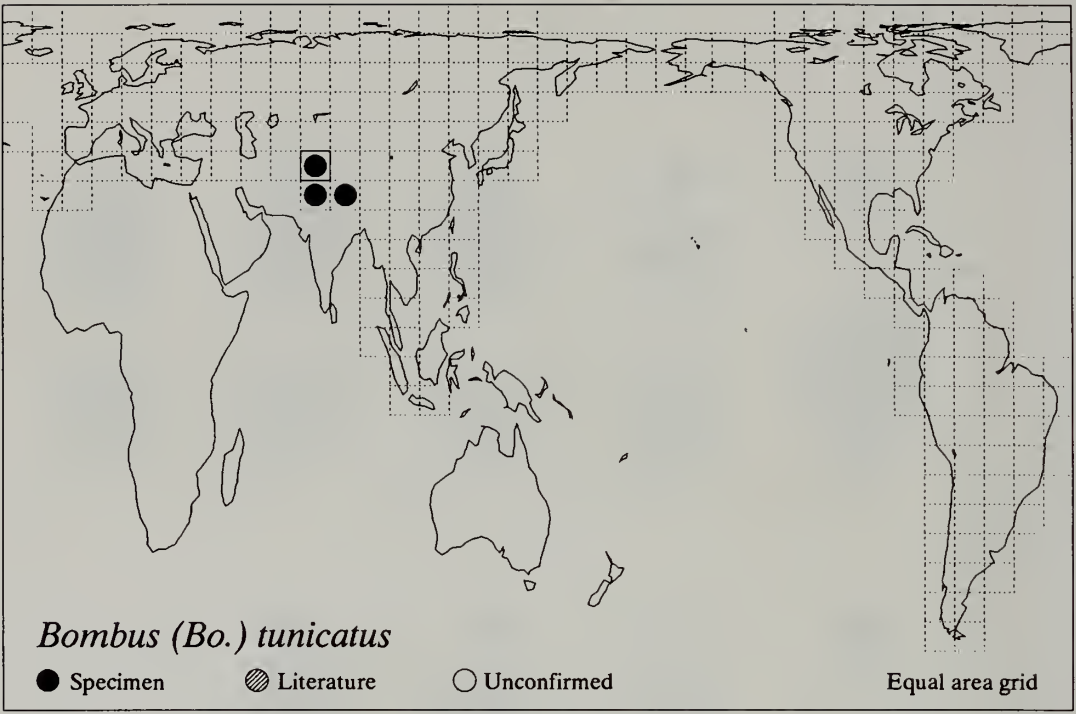
Map 41 Summary of the world-wide distribution of *B. biroi* (for an explanation of the symbols see Map 5).



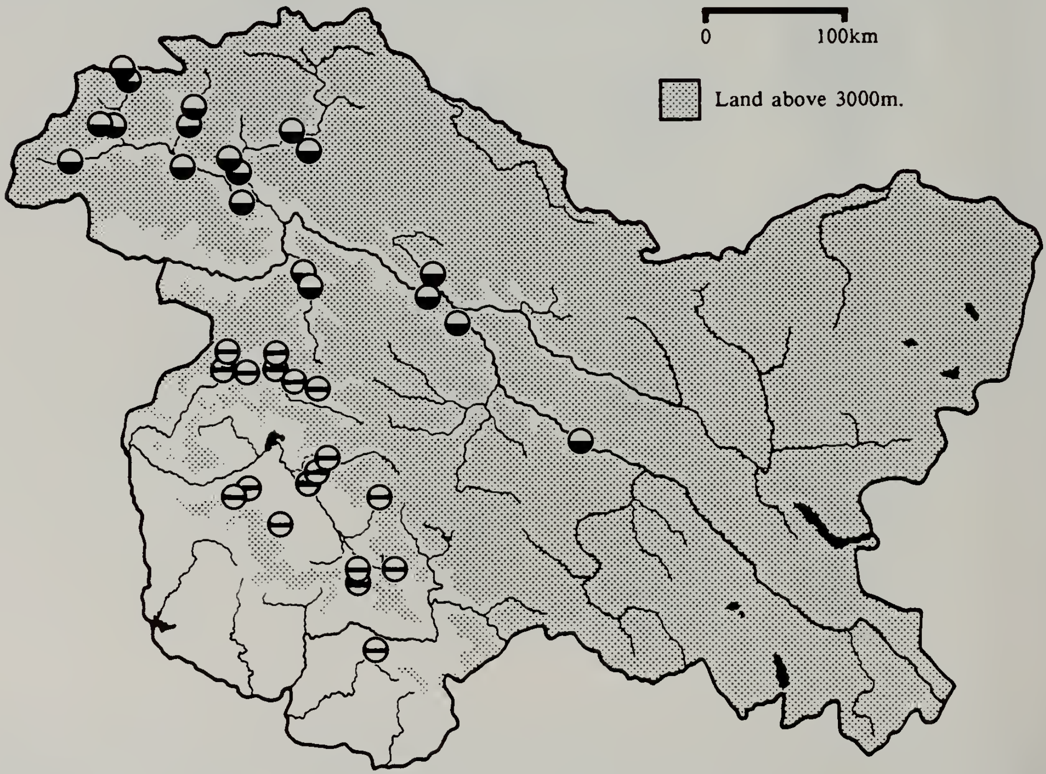
Map 42 Distribution of *B. biroi* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 335–346).



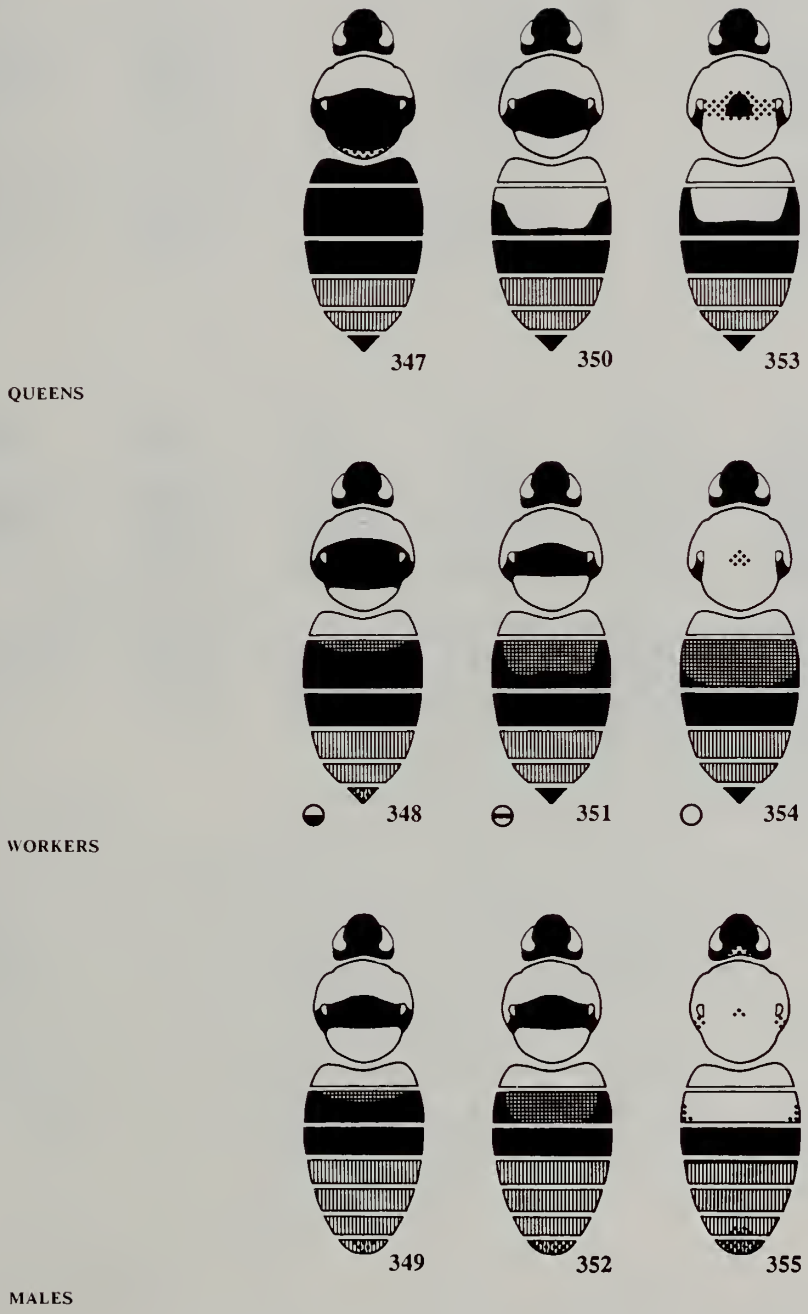
Figs 335–346 Colour patterns of *B. biroi* from localities in Kashmir: (335) Chhantir Gah 5–7.viii.1954, (336) Rumbak 12.viii.1980, (337) Tungri, (338) Gumri 10–11.viii.1986, (339) Gumri 10–11.viii.1986, (340) Gumri 30.ix.1986, (341) Apharwat 25.vii.1986, (342) Apharwat viii–ix.1986, (343) Apharwat 23.viii.1985, (344) Apharwat 25.vii.1986, (345) Apharwat 15.viii.1980, (346) Apharwat 29.vii.1986 (for the colour key see Fig. 258).



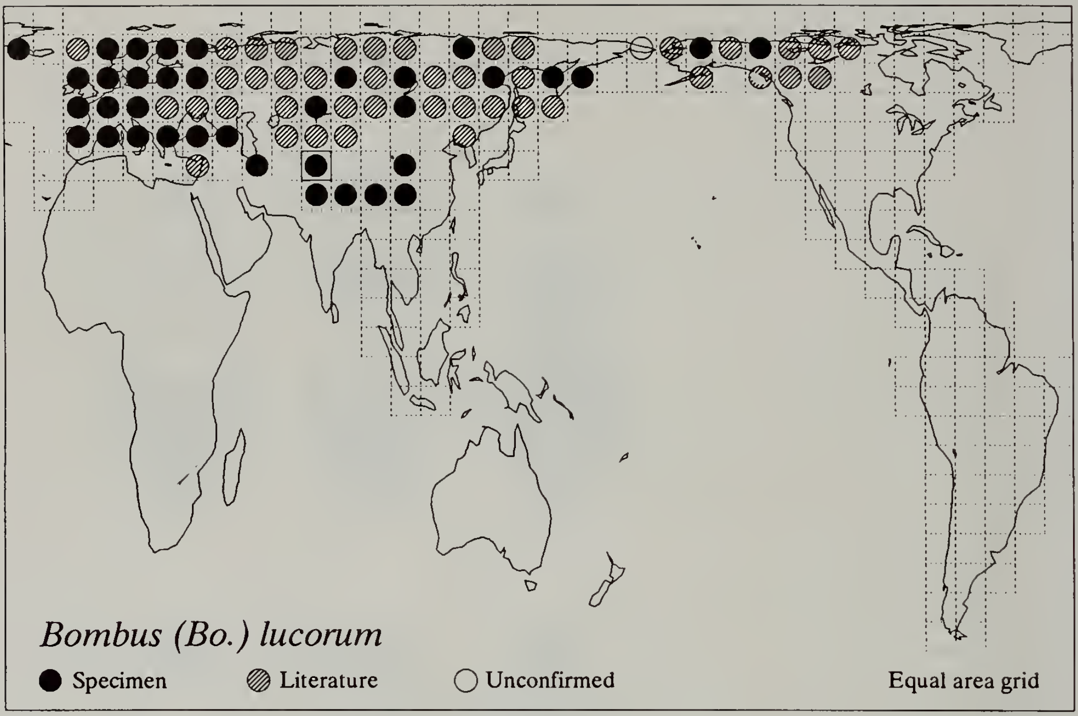
Map 43 Summary of the world-wide distribution of *B. tunicatus* (for an explanation of the symbols see Map 5).



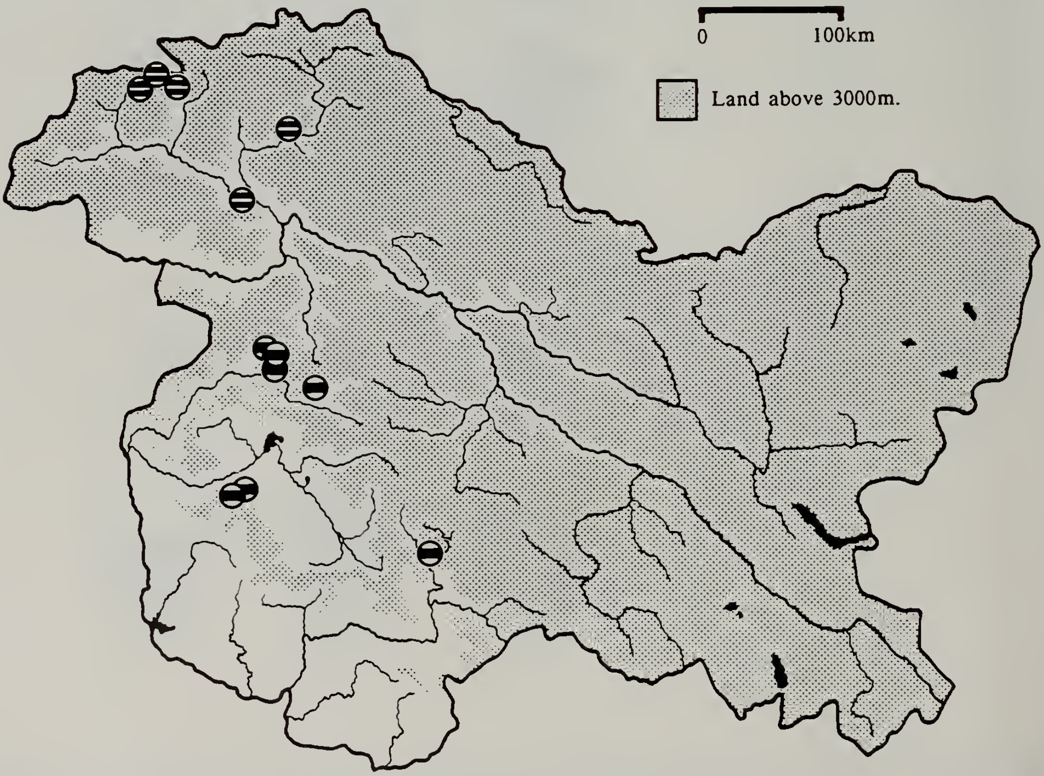
Map 44 Distribution of *B. tunicatus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 347–355).



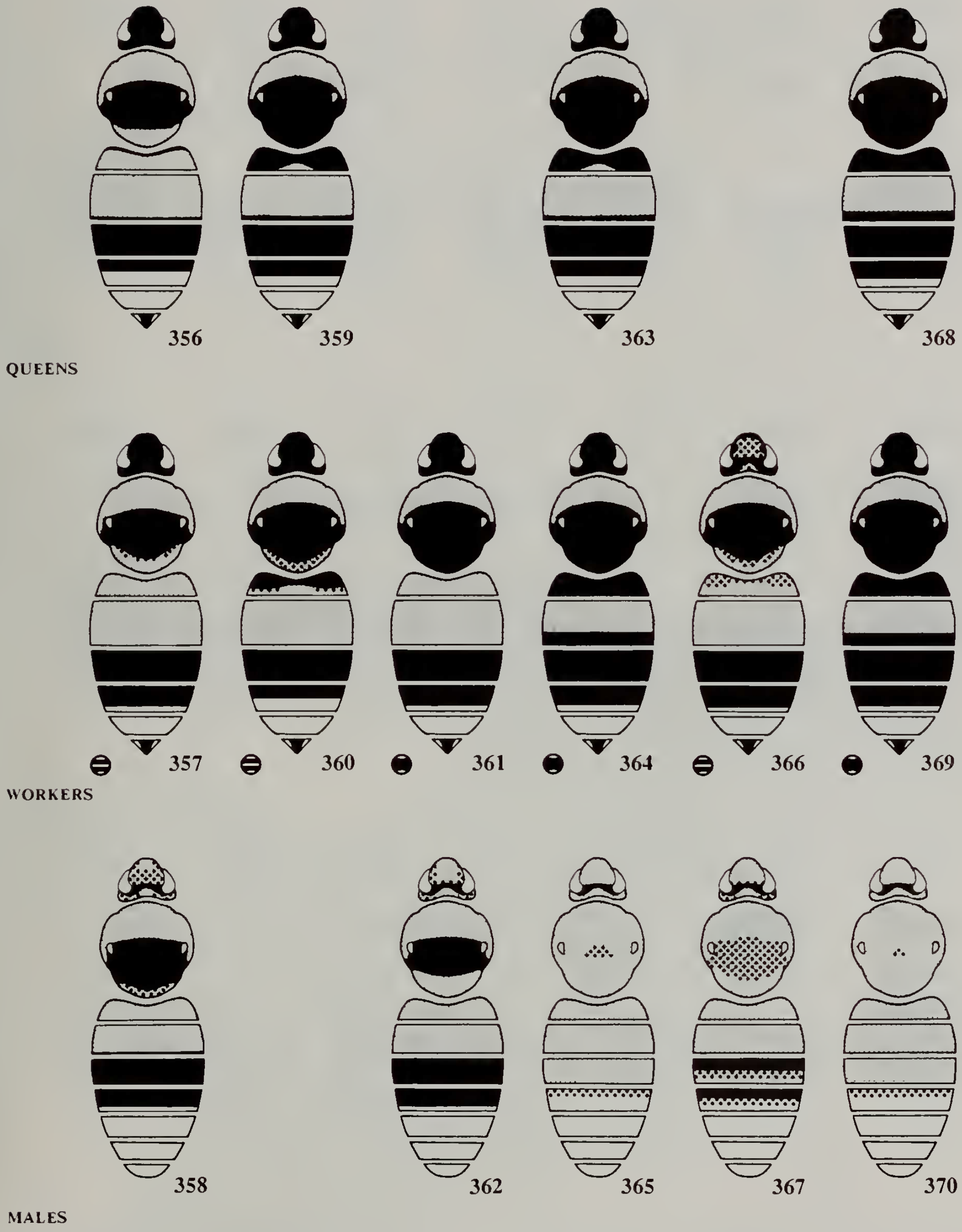
Figs 347–355 Colour patterns of *B. tunicatus* from localities in Kashmir: (347) Luskum 30.v.1954, (348) Gilgit vi.1954, (349) Shigar 1–3.x.1953, (350) Gulmarg vii–viii.1986, (351) Gulmarg viii.1986, (352) Gulmarg viii.1985, (353) Gulmarg vii–viii.1986, (354) Gulmarg 10.viii.1980, (355) Gulmarg viii–ix.1986 (for the colour key see Fig. 258).



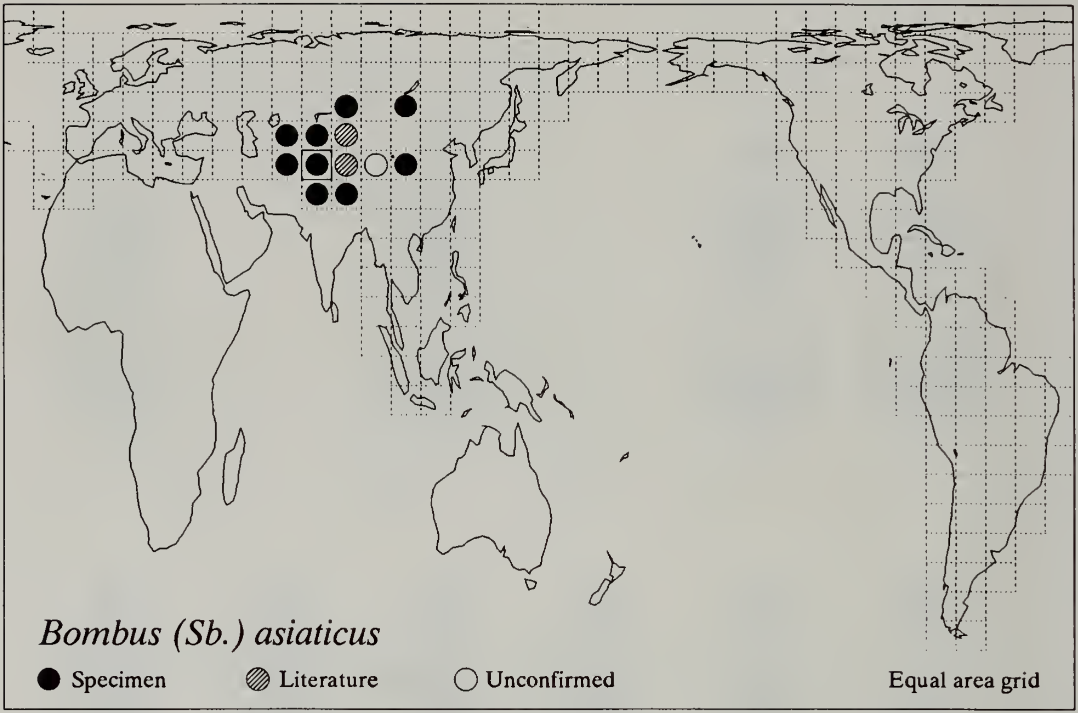
Map 45 Summary of the world-wide distribution of *B. lucorum* (for an explanation of the symbols see Map 5).



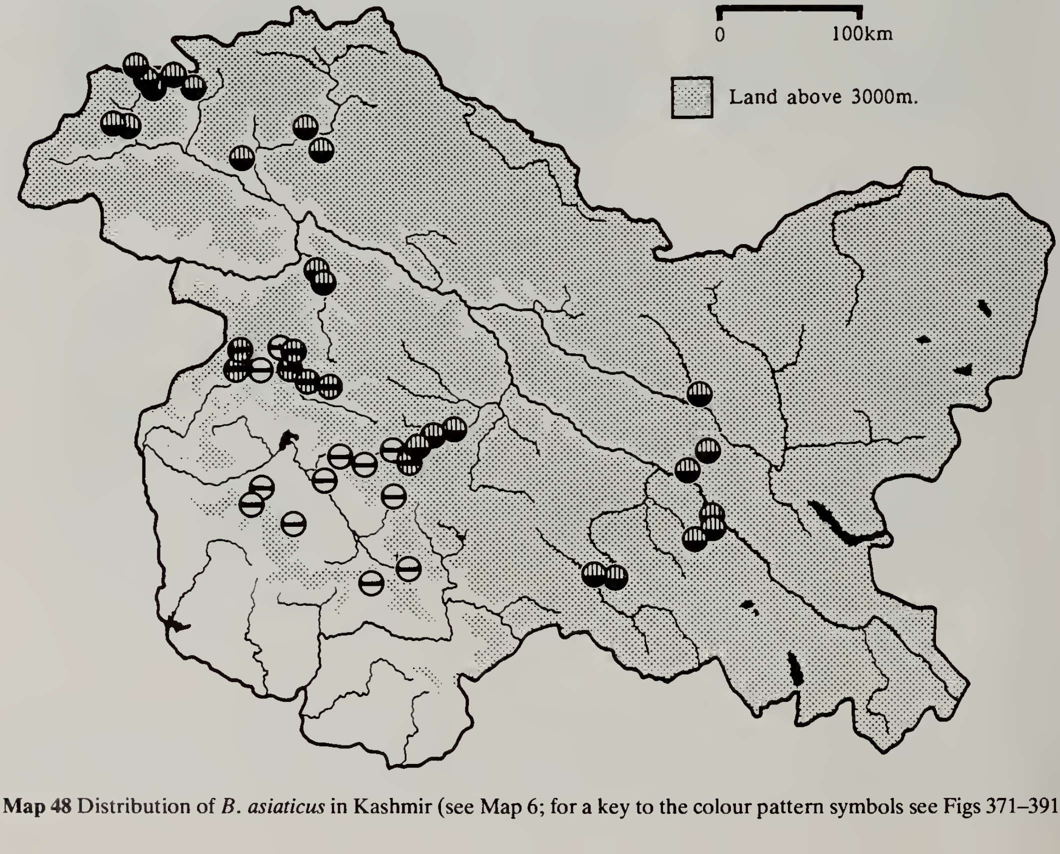
Map 46 Distribution of *B. lucorum* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 356–370).



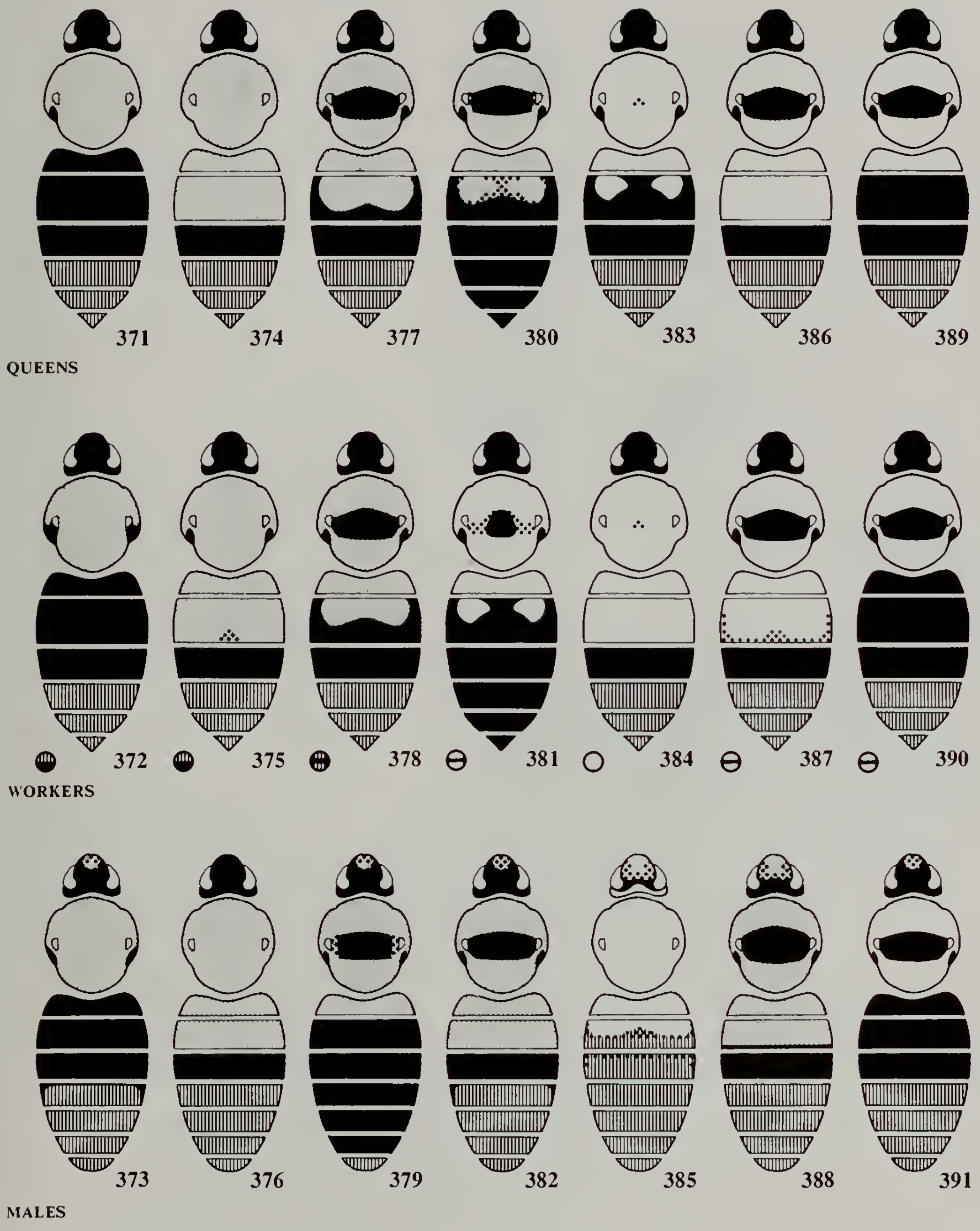
Figs 356–370 Colour patterns of *B. lucorum* from localities in Kashmir: (356) Baltit 14–17.vi.1954, (357) Baltit 14–17.vi.1954, (358) Baltit 15.viii.1913, (359) Baltit 14–17.vi.1954, (360) Atro Sar 11.viii.1954, (361) Chittakatha Sar 19–24.viii.1954, (362) Lal Pani 2–3.ix.1953, (363) Maru 19.v.1910, (364) Lal Pani 2–3.ix.1953, (365) Lal Pani 2–3.ix.1953, (366) Apharwat 30.viii.1986, (367) Apharwat viii.1985, (368) Apharwat 17.vii.1986, (369) Apharwat 16.viii.1980, (370) Apharwat viii.1985 (for the colour key see Fig. 258).



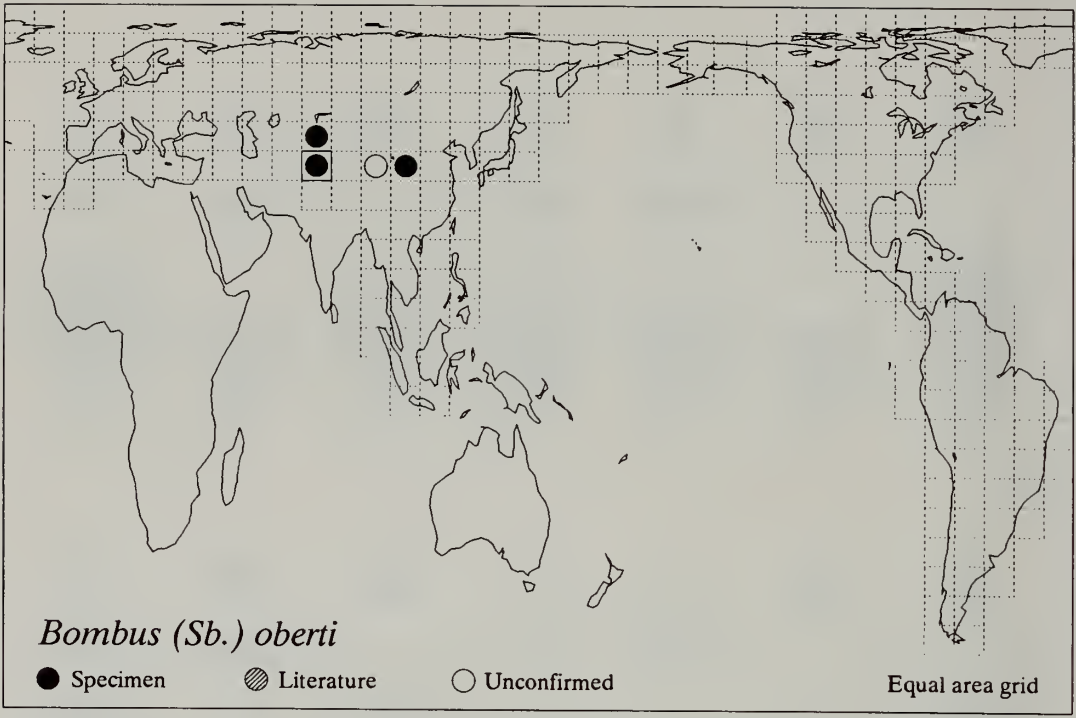
Map 47 Summary of the world-wide distribution of *B. asiaticus* (for an explanation of the symbols see Map 5).



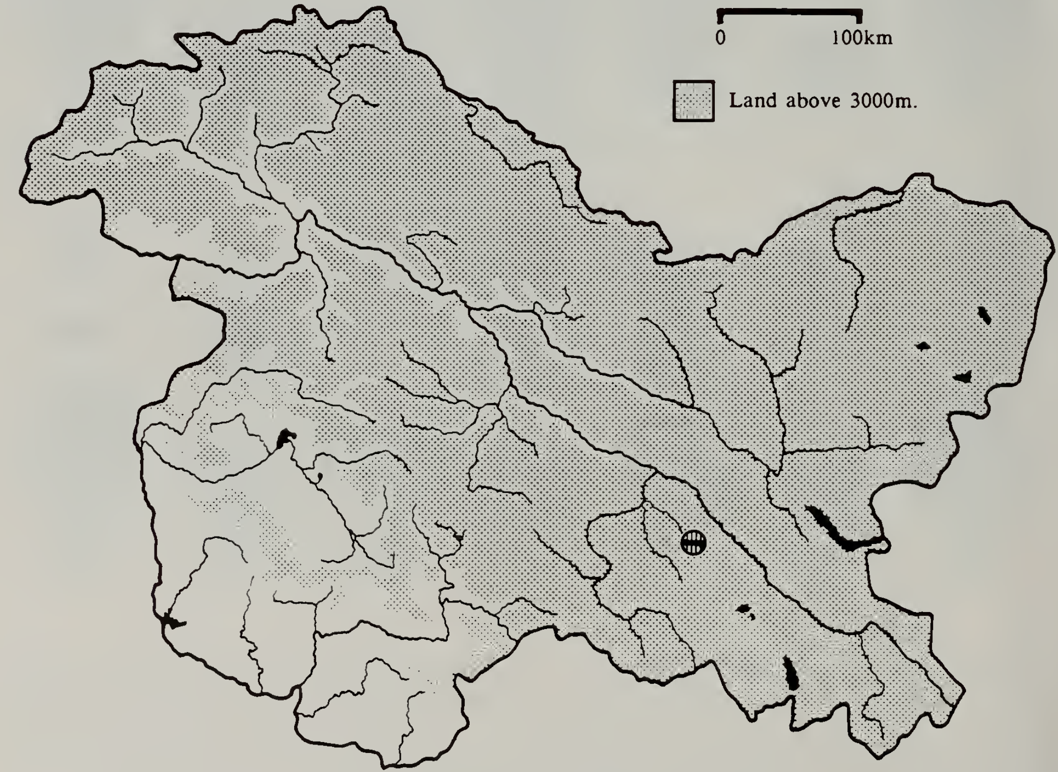
Map 48 Distribution of *B. asiaticus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 371–391).



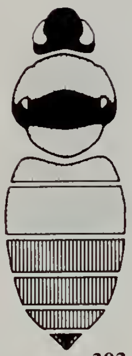
Figs 371–391 Colour patterns of *B. asiaticus* from localities in Kashmir: (371) Leh 19–27.ix.1986, (372) Leh 8.vii.1980, (373) Leh 19–27.ix.1986, (374) Thonde 1980, (375) Leh 3.vii.1980, (376) Thonde 1980, (377) Nigagar 17.ix.1986, (378) Nigagar 9.viii.1986, (379) Nigagar 17.ix.1986, (380) Lal Pani 2–3.ix.1953, (381) Lal Pani 2–3.ix.1953, (382) Lal Pani 2–3.ix.1953, (383) Gulmarg viii.1985, (384) Gulmarg viii.1985, (385) Gulmarg 29.viii.1986, (386) Gulmarg viii.1985, (387) Gulmarg viii.1985, (388) Gulmarg 12.viii.1980, (389) Yusmarg 8.ix.1985, (390) Gulmarg viii.1985, (391) Gulmarg 12.viii.1980 (for the colour key see Fig. 258).



Map 49 Summary of the world-wide distribution of *B. oberti* (for an explanation of the symbols see Map 5).



Map 50 Distribution of *B. oberti* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 392 & 393).



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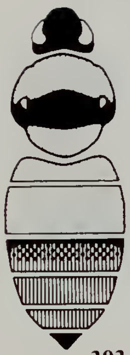

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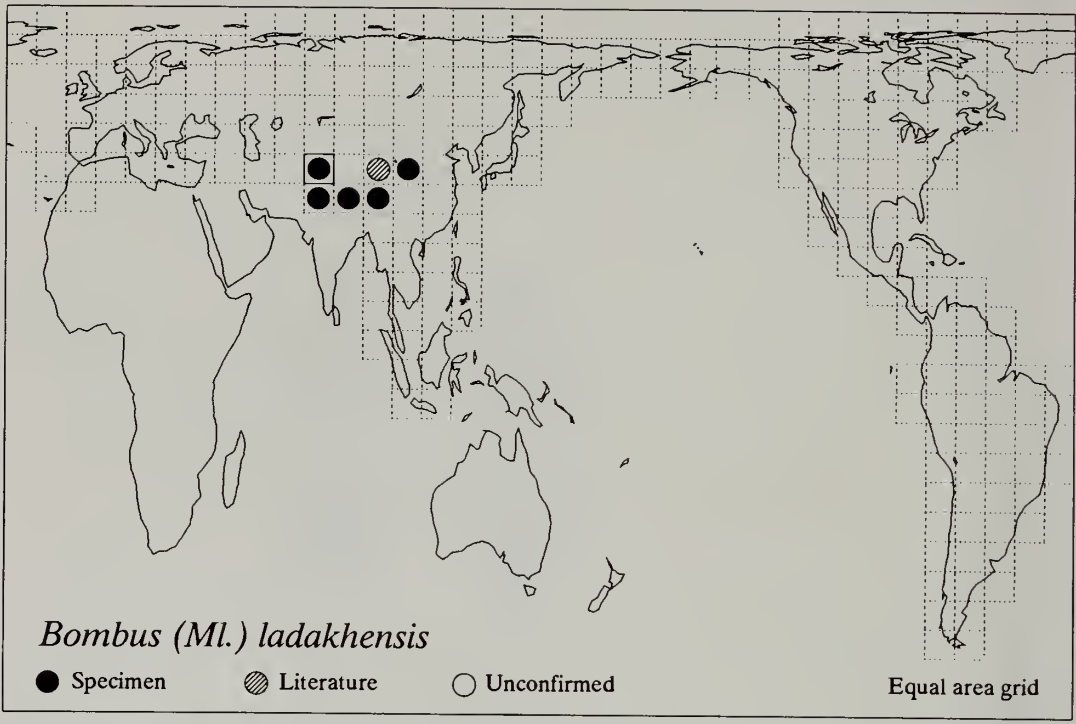
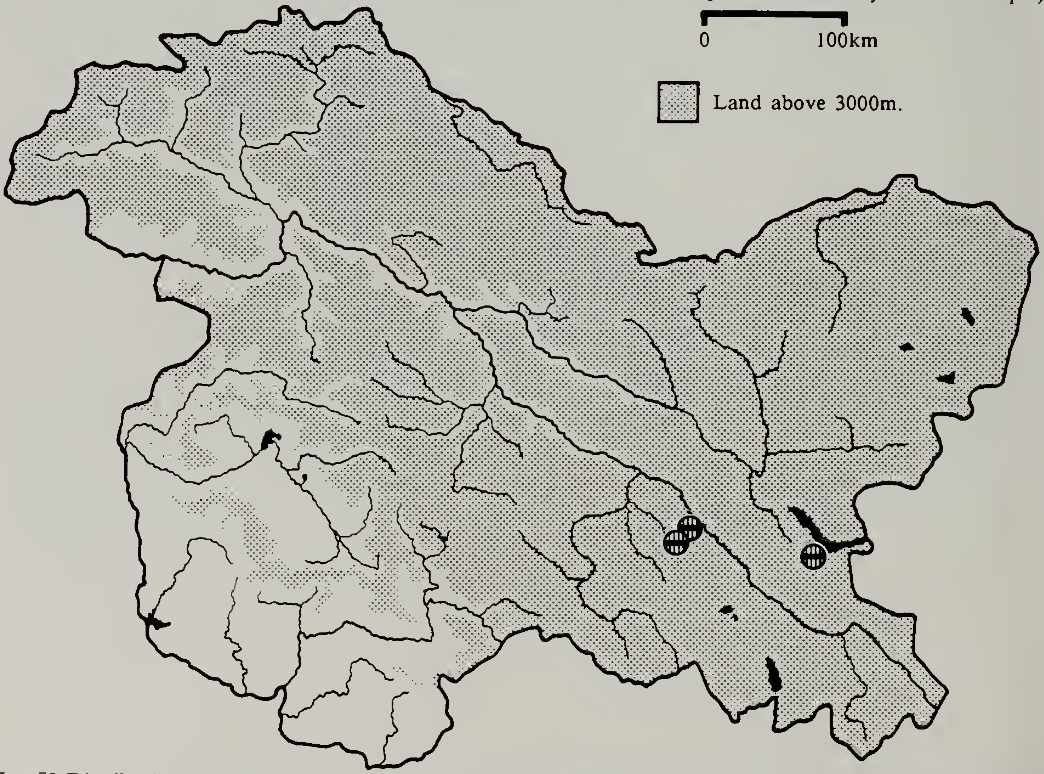
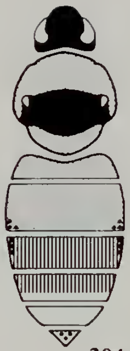
Figs 392, 393 Colour patterns of *B. oberti* from Kashmir: (392) Nimaling 15.vii.1980, (393) Nimaling 20.vii.1980 (for the colour key see Fig. 258).



Map 51 Summary of the world-wide distribution of *B. ladakhensis* (for an explanation of the symbols see Map 5).



Map 52 Distribution of *B. ladakhensis* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 394–396).



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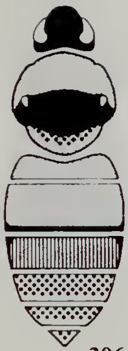

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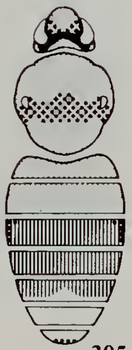

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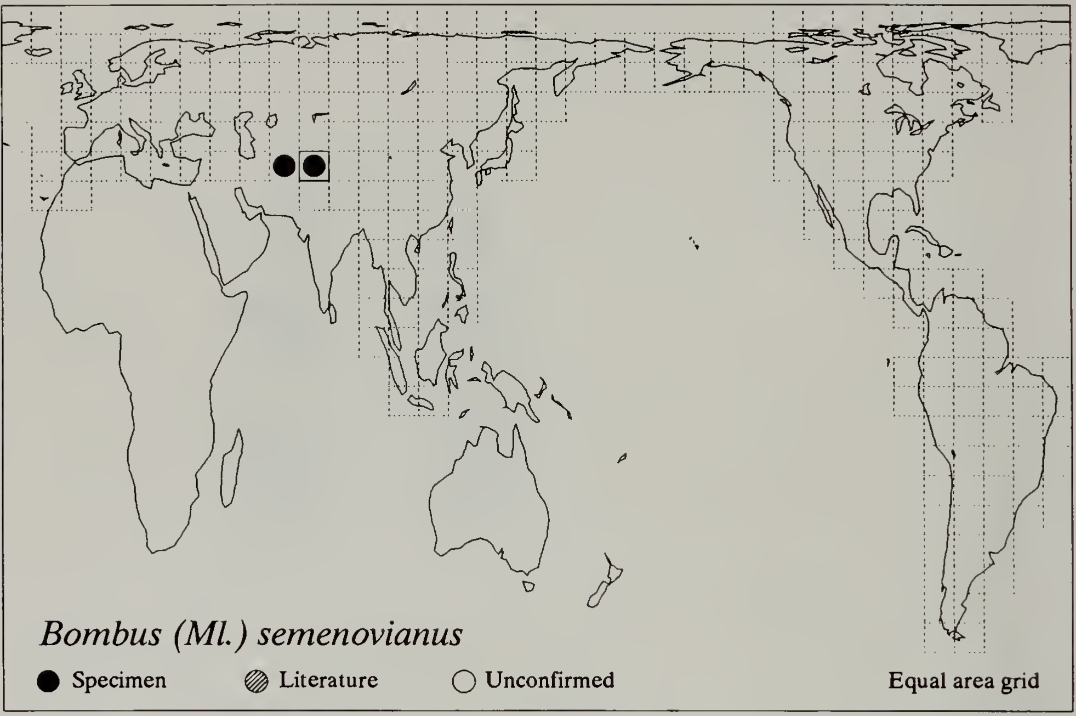
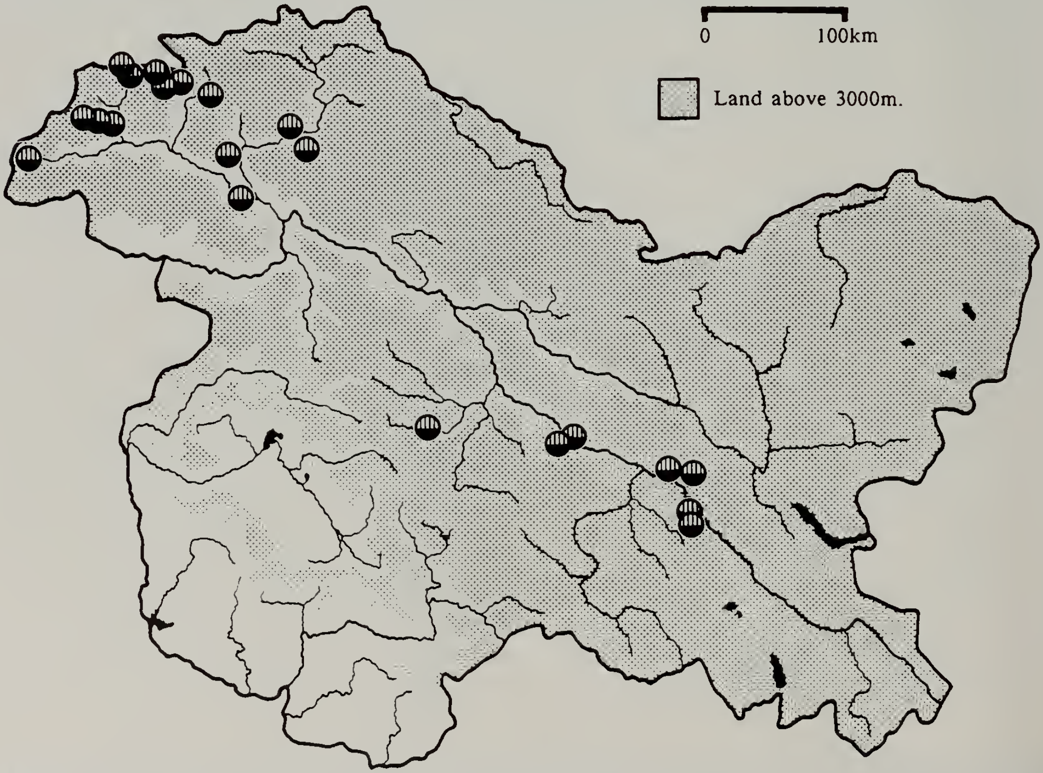
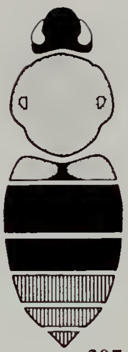


Map 53 Summary of the world-wide distribution of *B. semenovianus* (for an explanation of the symbols see Map 5).



Map 54 Distribution of *B. semenovianus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 397–402).



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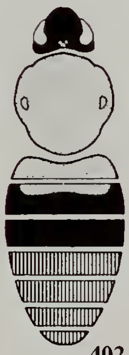

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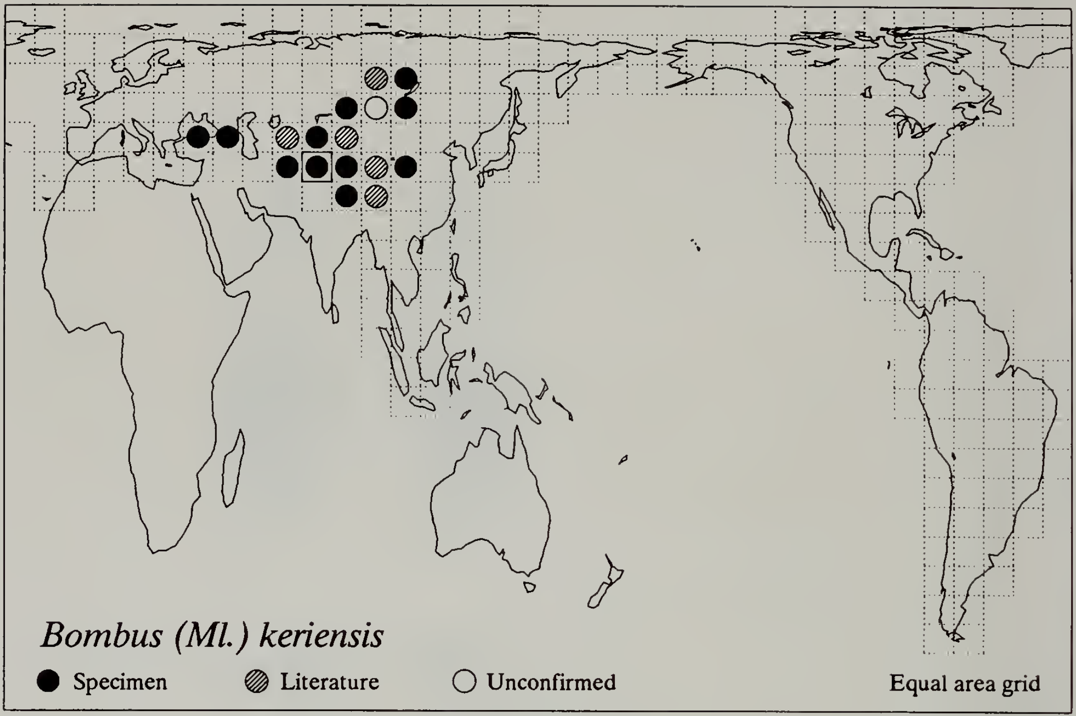
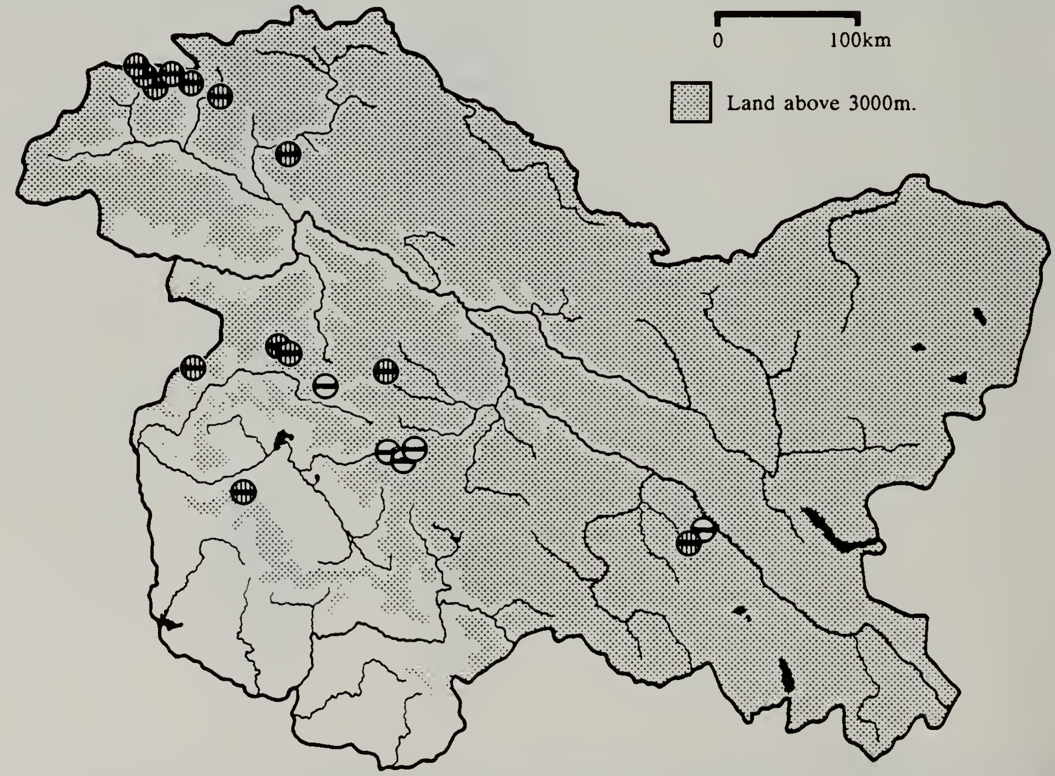
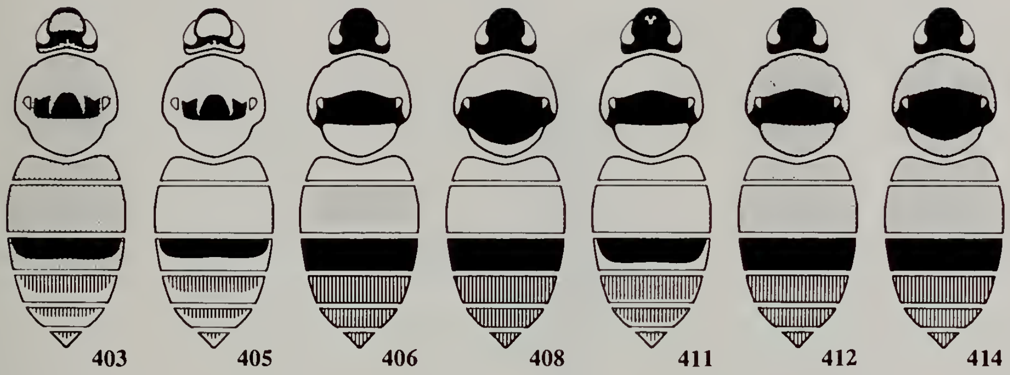
Figs 397–402 Colour patterns of *B. semenovianus* from localities in Kashmir: (397) Baltit 14–17.vi.1954, (398) Baltit 14–17.vi.1954, (399) Martselang 25.ix.1986, (400) Baltit 14–17.vi.1954, (401) Dras 10–11.viii.1986, (402) Hemis 25.ix.1986 (for the colour key see Fig. 258).



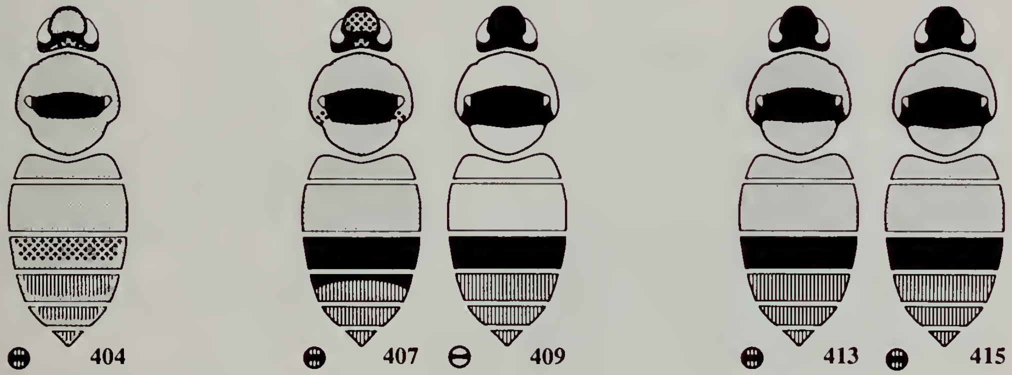
Map 55 Summary of the world-wide distribution of *B. keriensis* (for an explanation of the symbols see Map 5).



Map 56 Distribution of *B. keriensis* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 403–416).



QUEENS



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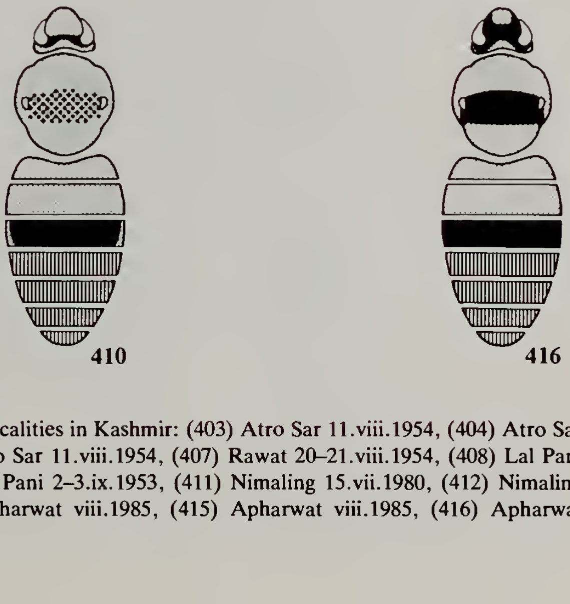

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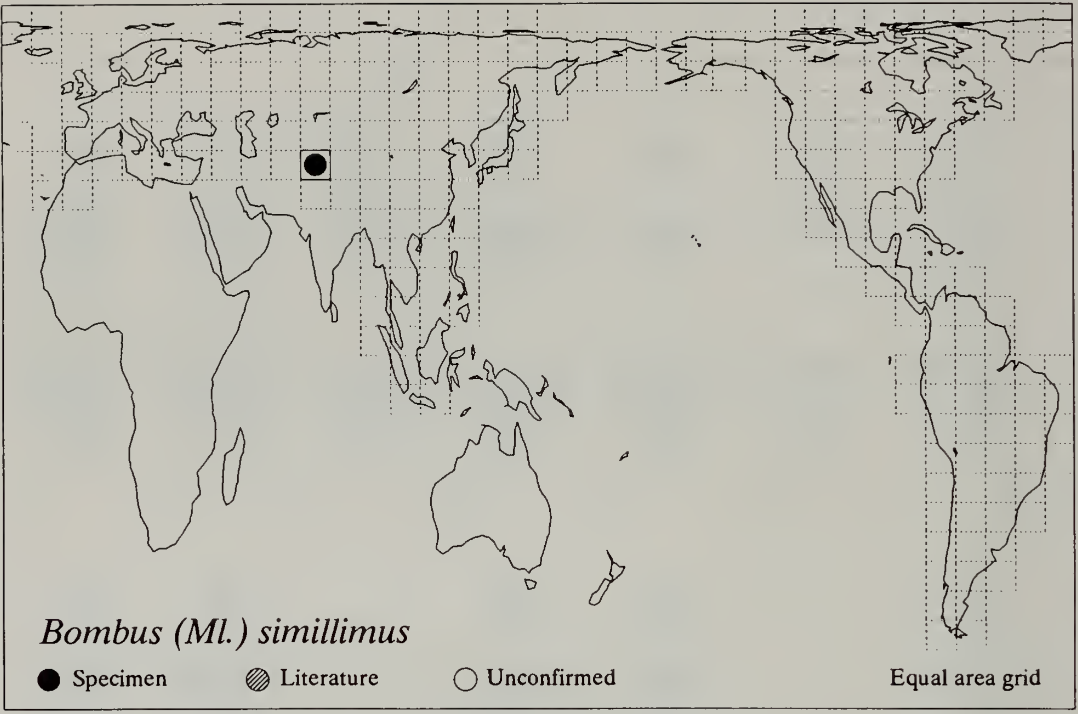
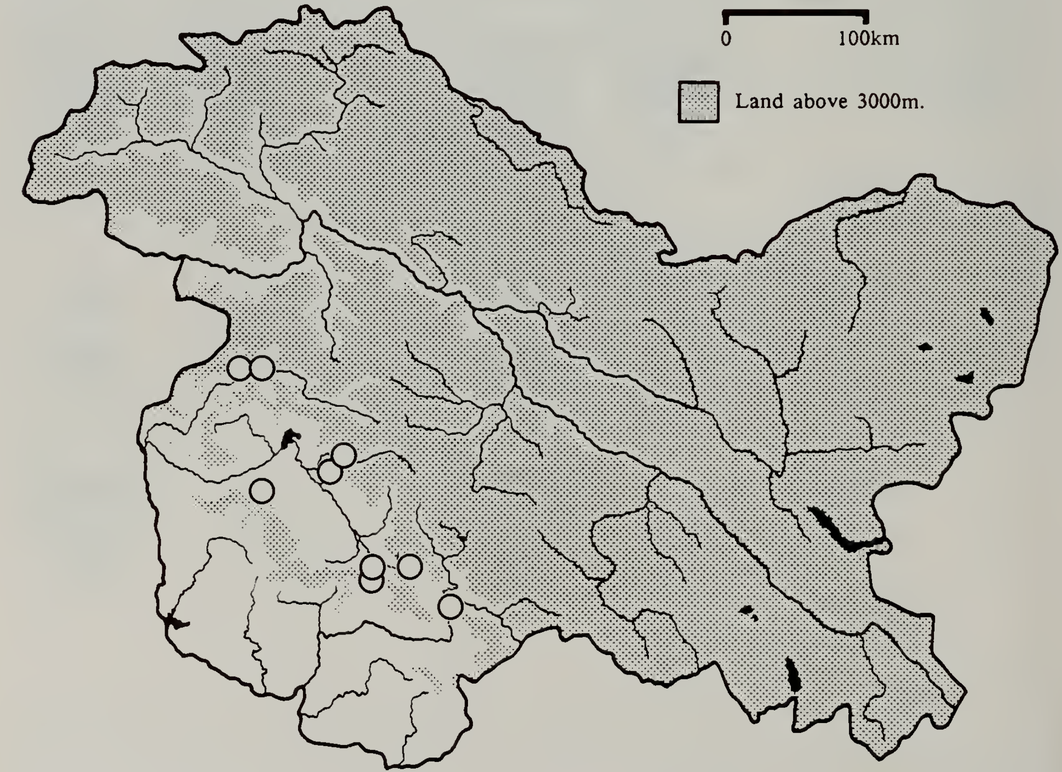
Figs 403–416 Colour patterns of *B. keriensis* from localities in Kashmir: (403) Atro Sar 11.viii.1954, (404) Atro Sar 11.viii.1954, (405) Atro Sar 11.viii.1954, (406) Atro Sar 11.viii.1954, (407) Rawat 20–21.viii.1954, (408) Lal Pani 2–3.ix.1953, (409) Lal Pani 2–3.ix.1953, (410) Lal Pani 2–3.ix.1953, (411) Nimaling 15.vii.1980, (412) Nimaling 15.vii.1980, (413) Nimaling 24.vii.1980, (414) Apharwat viii.1985, (415) Apharwat viii.1985, (416) Apharwat 23.viii.1985 (for the colour key see Fig. 258).



Map 57 Summary of the world-wide distribution of *B. simillimus* (for an explanation of the symbols see Map 5).



Map 58 Distribution of *B. simillimus* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 417–421).

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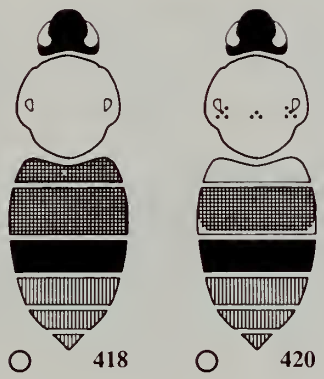

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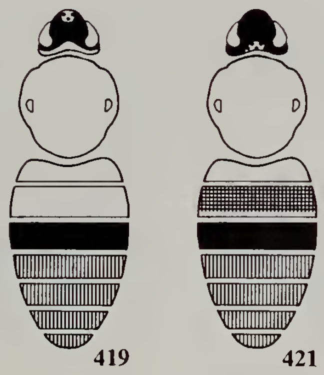

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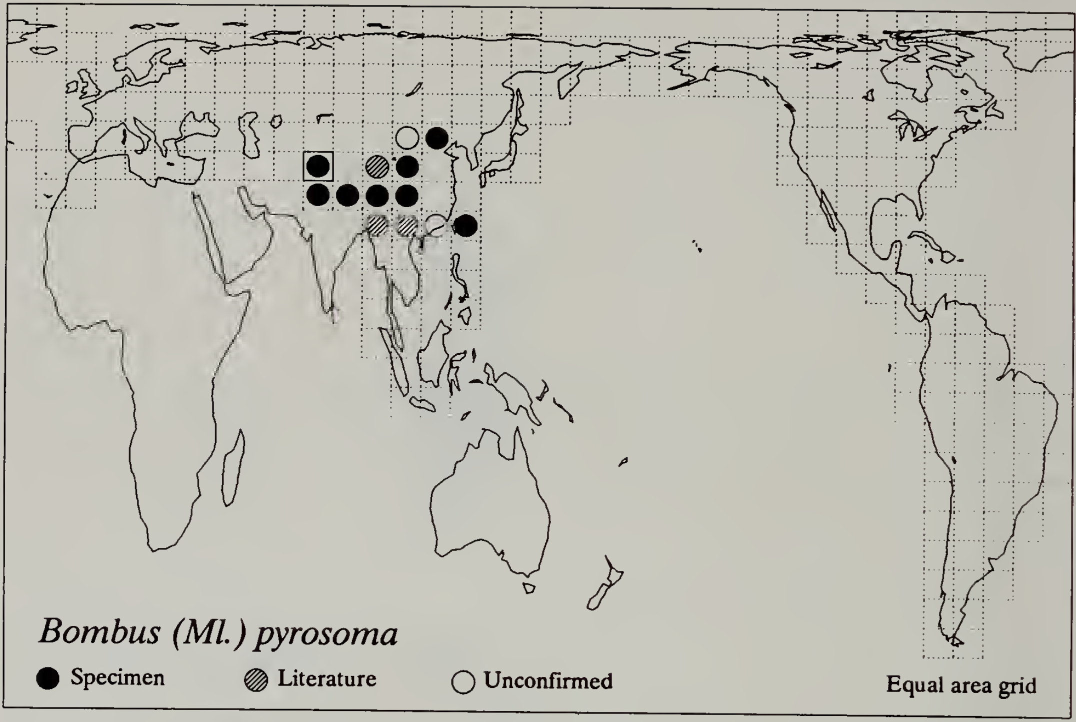
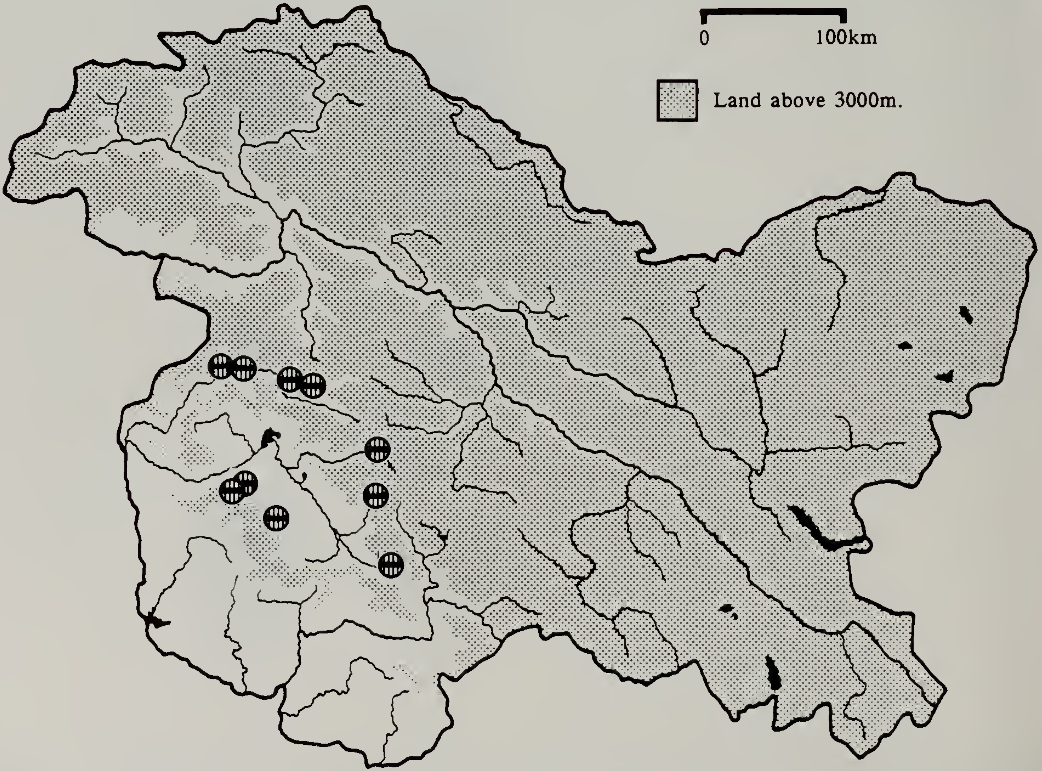
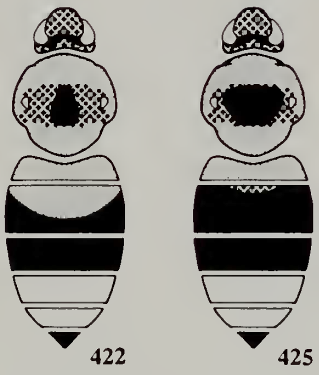
Figs 417–421 Colour patterns of *B. simillimus* from localities in Kashmir: (417) Harwan 10.ix.1985, (418) Harwan 10.ix.1985, (419) Harwan 10.ix.1985, (420) Harwan 10.ix.1985, (421) Banihal 3.ix.1986 (for the colour key see Fig. 258).



Map 59 Summary of the world-wide distribution of *B. pyrosoma* (for an explanation of the symbols see Map 5).



Map 60 Distribution of *B. pyrosoma* in Kashmir (see Map 6; for a key to the colour pattern symbols see Figs 422–430).



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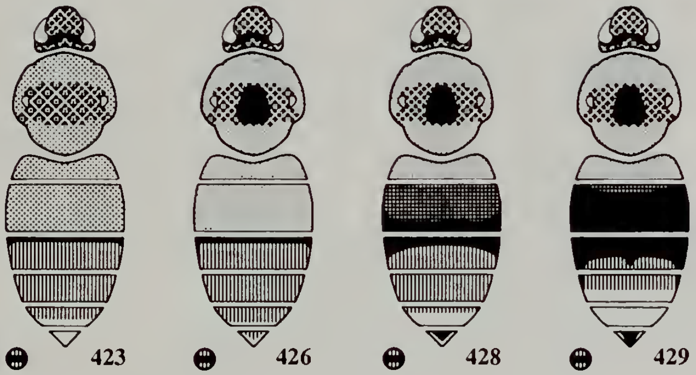

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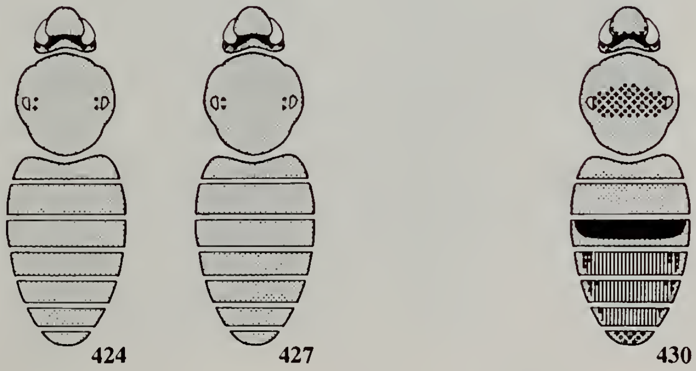

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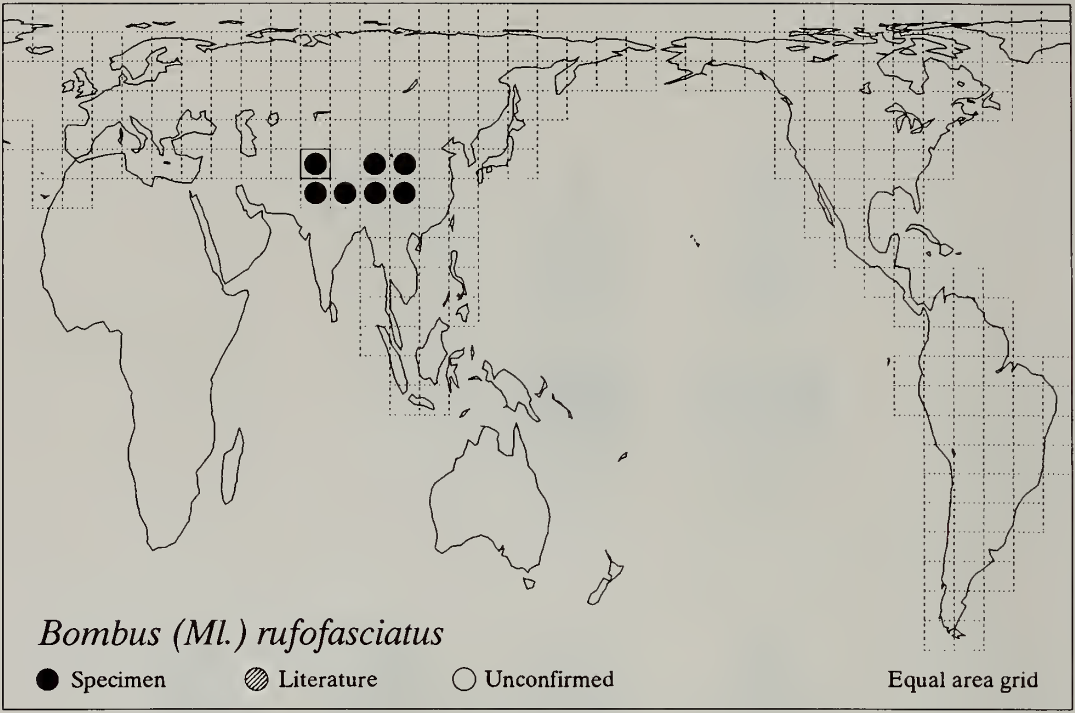
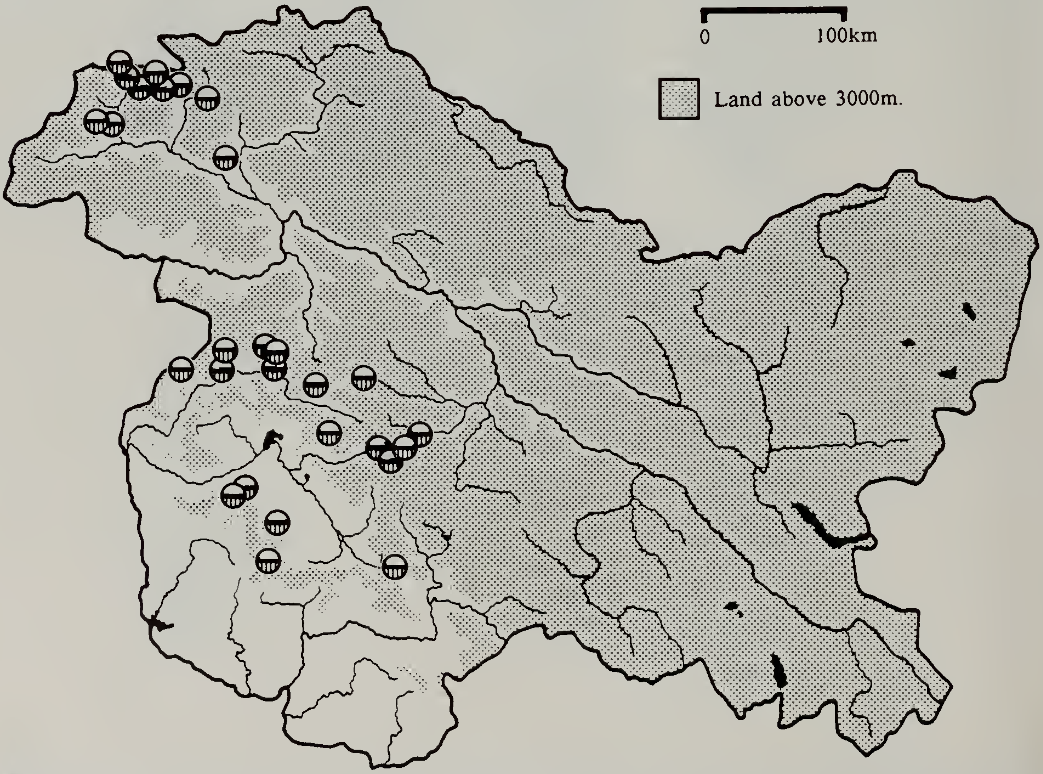
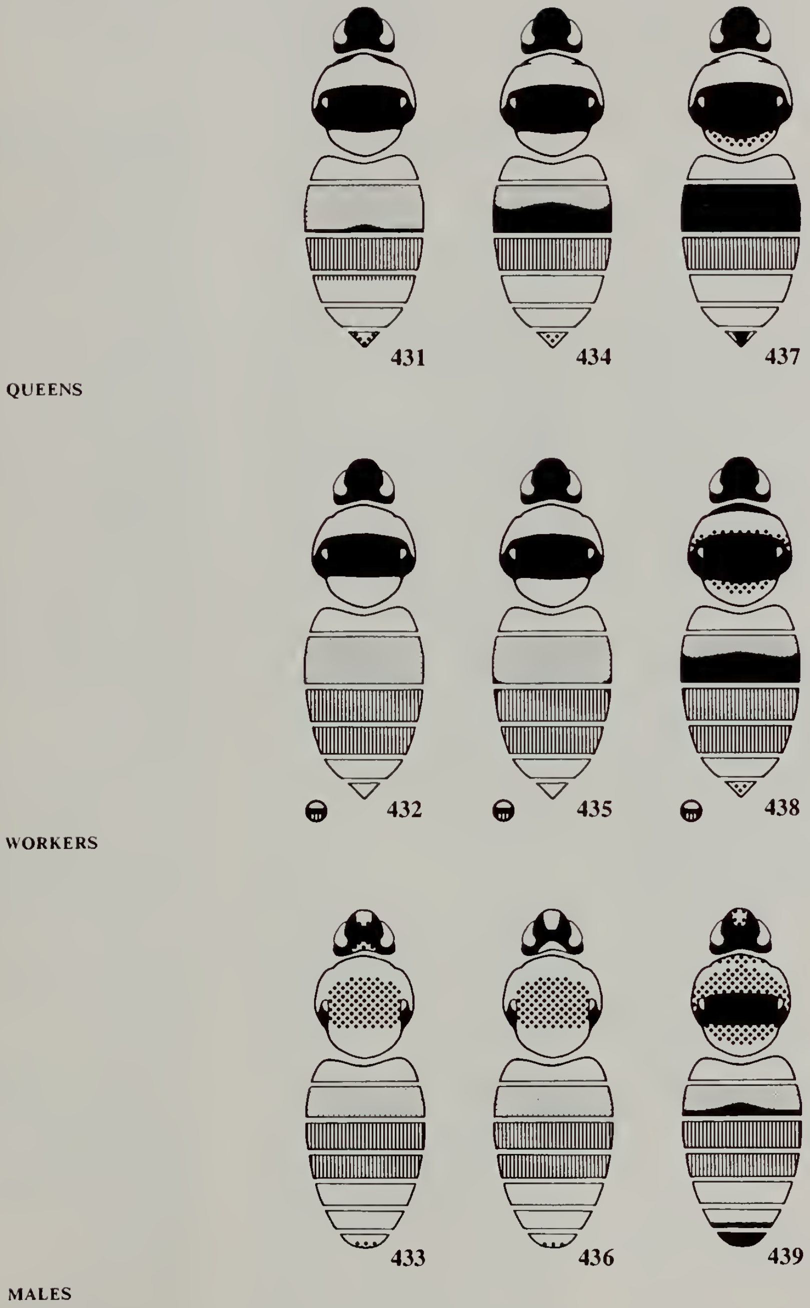
Figs 422–430 Colour patterns of *B. pyrosoma* from localities in Kashmir: (422) Kel 16.viii.1953, (423) Kel 16.viii.1953, (424) Kel 16.viii.1953, (425) Gulmarg 2.ix.1985, (426) Gulmarg viii.1985, (427) Apharwat 14.ix.1986, (428) Gulmarg viii.1985, (429) Gulmarg viii.1985, (430) Apharwat 14.ix.1986 (for the colour key see Fig. 258).



Map 61 Summary of the world-wide distribution of *B. rufofasciatus* (for an explanation of the symbols see Map 5).



Map 62 Distribution of *B. rufofasciatus* in Kashmir (see Map 6; for a a key to the colour pattern symbols see Figs 431–439).



Figs 431–439 Colour patterns of *B. rufofasciatus* from localities in Kashmir: (431) Atro Sar 11.viii.1954, (432) Atro Sar 11.viii.1954, (433) Rawat 20–21.viii.1954, (434) Apharwat 23.viii.1985, (435) Apharwat viii–ix.1986, (436) Apharwat viii.1985, (437) Apharwat 24.vii.1986, (438) Apharwat viii.1985, (439) Apharwat viii.1985 (for the colour key see Fig. 258).

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